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MULTI-RESOURCE ECOSYSTEM MODEL REVIEW : ECOSYSTEM PROCESS MODELS

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Multi-resource Ecosystem Model Review: Ecosystem Process Models

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Introduction

Purpose

In order to provide a review of computer ecosystem process models for forest pest managers and forest managers in general, a literature review of has been carried out. This document will define and classify these models, summarize an example from each major class of ecosystem process models, provide information pertaining to the input requirements and output of various ecosystem process models, and include an extensive bibliography of ecosystem process models.

Types of Models

The term "model" has many connotations which are summarized below. This summary largely follows the logic of Kimmins (1987). This will clarify what is meant by a "computer model" and an "ecosystem process model" and provide a context for the discussion that follows. This context is particularly important for ecosystem process models which are used to test conceptual models of ecosystem function, as well as to produce predictions of future ecosystem properties.

Conceptual models

Conceptual models have existed for millennia either as personal cerebral explanations of natural phenomena, or as written and oral explanations of those phenomena. Conceptual models are necessarily limited by a person's ability to simultaneously consider multiple causes and effects of events. Scientific papers generally present their findings within the framework of a conceptual model and may support or refute various aspects of currently accepted conceptual models.

Graphic models

Graphic models grow out of conceptual models and come in many forms. They may be three-dimensional as the case of the physical models commonly used in engineering. Two-dimensional models include pictures, flowcharts and graphs. Pictures may be aesthetically pleasing, but graphs describing relations between two or among three variables provide a clearer representation of empirical relations and the scatter associated with them. When many processes interact, the shortcomings of conceptual models may be mitigated with flowcharts including all processes considered to be relevant. Engineers first provided the basis for systems analysis (Logan 1994) and an electrical engineer by the name of Forrester (1961) presented a useful standard for flowcharts (they are often referred to as Forrester diagrams). Flowcharts combined with graphs can support conceptual models in a compelling manner, however descriptions of ecosystem function under various treatments requires more rigor.

Mathematical models

Mathematical descriptions of natural phenomena provide the basis for computer models which simulate ecosystem processes. A mathematical description may be as simple as a linear relationship between variables, or it may be a large set of second or higher order non-linear differential equation which includes interacting multiple feedback loops among various processes. Further, a mathematical description of a system may be deterministic or stochastic (includes natural variability). Finally, a distinction should be made between equations which merely demonstrate an empirical correlation (e.g. tree age and diameter at breast height (dbh), and those which attempt to describe an actual process at a mechanistic level (e.g. temperature-dependence of the gross photosynthesis rate of a particular species). Natural systems are so complex that a few equations are not sufficient to predict their function and structural changes under various treatments, natural disturbances, and climate change. Flowcharts provide clarity that a simple set of equations cannot. The combination of equations and flowcharts create the rigor necessary to produce computer models from conceptual models.

Computer models

Mathematical models can be coded into computer language, converting differential equations to simpler finite-difference equations which approximate differential equations when the time step is small. This allows a machine to do the routine but immensely numerous calculations. The size, availability, and cost of computer time is only one limit on the complexity of these models. The art of modeling is apparent when decisions are made about which processes to include in the model. If the purpose is to accurately mimic the natural function of a system, it is not always appropriate to include the greatest possible number of variables. O'Neill (1971) described the reduction of model inaccuracy as an optimization process. Increasing the complexity of the model theoretically increases our ability to simulate a system, however each additional parameter carries with it additional parameterization error. Thus the ideal model may not be the most complex. For the purposes of this document, "computer model", "simulation model", and simply "model" will be used interchangeably to refer to the simultaneous solution of multiple equations on a digital computer. These terms will *not* refer to simple database management systems which simply facilitate the management of large amounts of interrelated data, as included in John Silbaugh's companion document (hereafter referred to as Silbaugh 1995).

Types of Computer Models

Objectives of models

For this review, forestry computer models have been split by their objectives. On one hand, there are non-timber resource management models (fire, wildlife, hydrology, and recreation or scenic quality models as described in Silbaugh (1995), and on the other hand, there are ecosystem process models. In the past, forestry models have also been divided into two types, those that have prediction as their primary objective, and those that have understanding the system as their primary objective (Vanclay 1994). Many of the ecosystem process models fall into the latter category, with researchers developing them primarily to generate hypotheses. Where the model fails to match empirical evidence, an area for further research can often be identified. However, some of these models are becoming refined enough that they have predictive potential, particularly if used in a locale for which they are parametrized. This may be particularly true if a synergy can be created by combining them with pest management models. Note that not all ecosystem process models have hypothesis generation or ecosystem understanding as their primary goal. In particular, many of the gap models have reached a stage where they are being used in a predictive manner to project successional patterns. The role of computer models in hypothesis generation and management is presented in Figure 1. .

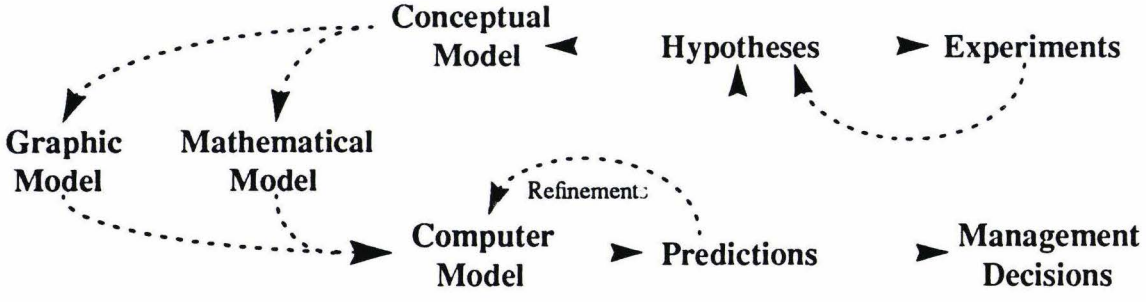

Figure 1. Computer models have become important tools in the scientific process, as experiments have always been. The heuristic value of ecosystem process models does not exclude their utility as management tools, however, particularly as individual models mature. Simplified from Kimmins 1987.

Ecosystem process model: A definition

An ecosystem process model is one which strives to explicitly and mathematically describe fundamental biological and/or ecological processes, and then scales up to at least the tree and usually the stand level or beyond. This working definition of ecosystem process models excludes many resource management models as well as the traditional empirical growth and yield models. In this document, some growth and yield models will be mentioned to provide a broader context for other models. The definition is a subset of a category described by Kimmins (1987) wherein modelers forego mathematical elegance in an effort to make the best possible description of the biological

attributes of a system. In reality, models fall along a continuum between this extreme and another wherein biological details are ignored in the pursuit of theoretical and mathematical elegance. Ecosystem process models can be organized further by the spatial resolution of the processes simulated, spatial resolution of the simulations performed, temporal resolution (time-step), and other characteristics (Figure 2).

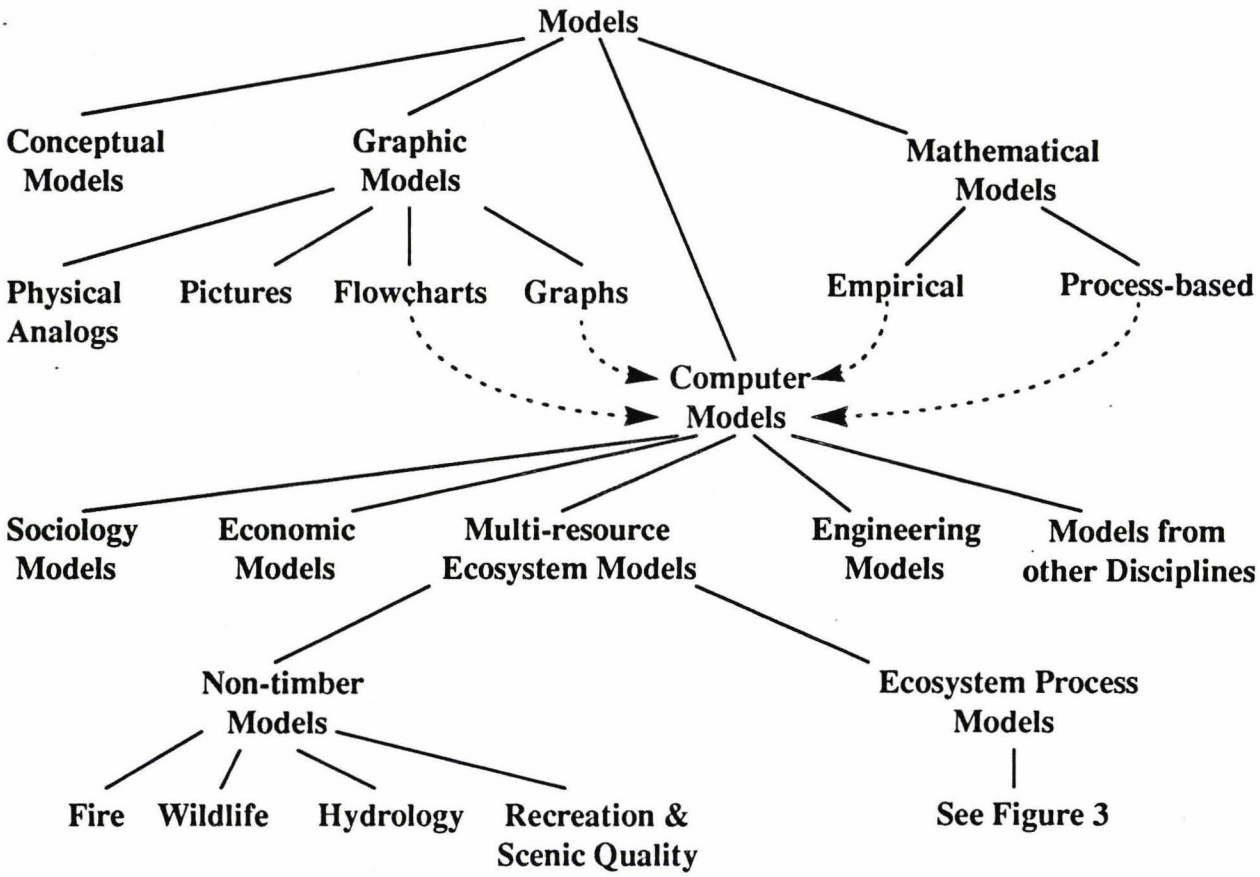

Figure 2. Ecosystem process models are a subset of computer simulation models which in turn are the products of several other types of models.

Examples of Model Classes

Examples from each of the four model classes will be used to demonstrate some of the details of a model or two in each class of models. These will include FOREST-BGC, BIOME-BGC, JABOWA, FORET, CENTURY-*forest*, and TEM. Information on other models is provided in Appendix A: Characteristics of Selected Models.

Bibliography of Computer Simulation Models

A primary goal of this review was to compile a compendium of citations relating to computer simulation models (Appendix B). A preliminary literature search was conducted using the National

Agricultural Library Online Access (Agricola) database. This database was selected because of its long history (back to 1978) and the fact that it is in the public domain. An initial search brought up nearly five thousand sources pertaining to models. Less than seven hundred remained when these were sorted to include only those documents pertaining to ecosystem process models. Throughout the project, citations of pertinent documents were added to a master Reference Manager file whenever they were encountered. Each citation in the "Literature Cited" section and Appendix A, is also listed in the bibliography (Appendix C). Finally, any reference cited in Cooperative Agreement 28-C4-808, the associated Proposal for Cooperative Research, and Silbaugh (1995) are included in the bibliography. This brings the total number of citations to more than a thousand.

Abstracts and annotations are available for many of the citations. The abstracts are available from CAB Abstracts (Commonwealth Agricultural Bureau International) and secondarily from Biosis (Biological Abstracts, Inc.). CAB dates back to 1984 and is not published quarterly. CAB is not published quarterly, thus the January through March, 1995 Biosis database was reviewed. Several abstracts were typed into the database by hand as well, bringing the number of available abstracts to more than four hundred. This database is currently stored on a Reference Manager file that is searchable by keyword, author, title, journal, or year.

I used several criteria to determine if a citation should be included in the database. High priority documents included citations, with or without abstracts, of original publications describing ecosystem process or fully integrated regional models (described below), documents which reviewed one or several ecosystem process models, or those which had an application of an ecosystem process model as their centerpiece. Lower priority for inclusion were citations with abstracts of empirical models, pest models, conference proceedings, and articles that are not in English. Examples of citations not included in the database are those which do *not* have abstracts readily available and refer only to empirical models, pest models, are not in English, or pertain primarily to economic and sociological phenomena. References cited only in Appendix A: Characteristics of Selected Models are not included in "Literature Cited" but are included in appendix C: Bibliography.

Ecosystem Process Model Classification

A common categorization of ecosystem process models divides them by spatial resolution into four types; physiology-based models, population models, ecosystem/tissue models, and regional/global models (Ågren *et al.* 1991, Perruchoud and Fischlin 1994, Ryan 1995). The primary characteristic distinguishing these categories is the resolution of the processes described (e.g. biochemistry as

contrasted with climate data on a 0.5° x 0.5° global grid). The spatial application (single tree to global) of the models tends to vary with the resolution of the processes described in the model. For instance, models that include fine-scale mathematical descriptions of CO_2 and temperature-dependent C_4 photosynthesis are likely to be applied to a small patch of grassland and unlikely to be used on a global scale. The categorization is an artificial construct which takes a continuum of model types and divides them somewhat arbitrarily into the following four classes (Figure 3)

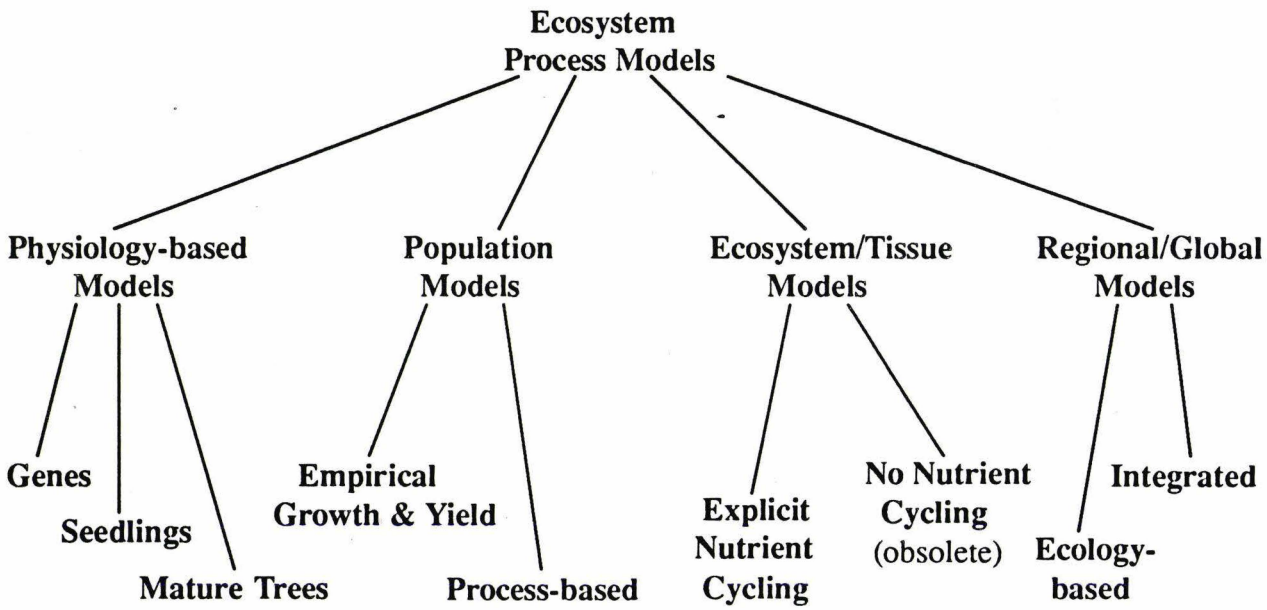

Figure 3. Classifications of ecosystem process models are often based on spatial scale and the processes explicitly in programmed into the model.

Physiology-based Models

The goal of physiology-based models is to scale up from micro-environment scale processes to the canopy level and beyond. The defining characteristic of this class of models is the explicit modeling of biochemical processes. Recent advances in physiological ecology have improved our understanding of leaf-level radiation balance, the trade-off between carbon assimilation and transpiration losses, respiration, plant nutrient requirements, and decomposition processes. This has allowed and necessitated the development of computer models to simulate leaf-level responses to varying environmental conditions. Modeling processes at this scale increases the predictive value of the results since they are less constrained by site-specific empirical growth data. However, challenges arise in parameterization of site climate data in regions that do not have readily available meteorological data. At least one model MT-CLIM, has been developed to extrapolate cli-

mate information across regions for the specific purpose of providing input climate files for a physiology-based model (Running *et al.* 1987). Physiology-based models can be divided into those that focus on seedling germination and growth and those that focus on mature tree physiology (Kiester 1988). Another subset of these models which we will not consider are those which focus on genetic characteristics of populations (*cf.* Knowe 1989, Huber 1994). An ever-increasing body of biochemical knowledge is being incorporated into these models as it becomes available.

For instance, photosynthesis submodels may simulate the effects of atmospheric carbon dioxide concentration in relation to humidity. For C_3 plants especially, open stomates are a trade-off between allowing CO_2 in and letting H_2O inadvertently escape. The physiology-based models explicitly include this effect, and some models have separate photosynthesis routines for C_4 plants. Consideration of the hydrologic cycle may be quite detailed, including canopy interception, snowpack accumulation and melting dynamics, infiltration, evaporation and transpiration. Typically, the sun angle and light extinction down through the canopy is calculated based on the canopy-level irradiance and foliage density. The biochemical response to varying levels of light are considered, either as an average, by splitting the leaves into sunlit or shaded, or by actual leaf angles (Ågren *et al.* 1991). Temperature effects on photosynthesis are considered, generally with an empirically based parabolic function peaking at some optimal temperature and reaching zero near freezing and approximately 40°C. Nutrient limitations may be included using explicit models of labile versus recalcitrant nutrient pools in the soil or more simply as the Rubisco or nitrogen concentration in the leaves.

Respiration is also explicitly modeled. Typically, the maintenance respiration is dependent on an exponential function of the temperature which defines a variable known as the Q_{10}. This is the change in respiration rate given a 10°C change in temperature (e.g. Q_{10}=2.0 means that the respiration rate will be twice as high at 25°C as at 15°C). Respiration of woody biomass is thought to be a more important part of mature forests and this may be simulated by consideration of different plant tissues separately or by considering the C:N ratio of tissues involved. Growth respiration is generally considered to be a fixed percentage of NPP. If maintenance respiration matches or exceeds gross photosynthesis, then growth respiration will be zero.

At the end of each time step, or in the case of dual-time step models, at the end of the longer time step, carbon is allocated to various plant tissues. This may be handled by maintaining a set root: shoot ratio or constant C:N ratio in various plant compartments. Some models may increase the root:shoot ratio in cases of nutrient limitation. Nitrogen and other nutrients may also be allocated. Litter production above-and below-ground are generally considered and treated differently de-

pending on the vegetation form (e.g. annual, deciduous, evergreen). Nutrient recycling prior to leaf abscission is often explicitly or implicitly included.

Once the litter has been released to the soil, varying levels of detail are used to model decomposition. One to five or more soil compartments may be include in a model. Models with multiple soil compartment models can explicitly simulate multiple nutrients in various forms such as labile carbohydrates, lignin, and soil organic matter. This allows simulation of long-term soil organic carbon dynamics. Decomposition dynamics and heterotrophic respiration generally are calculated as a function of temperature (using the exponential Q_{10} concept), and soil moisture content.

Population Models

Population models broaden the ecological scope of analysis to include population dynamics and competition. This often includes the birth, growth, and death of individual trees. The explicit inclusion of competition for resources was first accomplished by Newnham (1964). The models may utilize light use - carbon assimilation equations, but generally do not involve detailed biochemistry. These models usually keep track of changes in individual trees on a "tree list." A subset of this type of model represents many trees in the forest with each tree on the tree list. Considering individual trees can provide insight into the effect of species composition, horizontal and vertical spacing, and age structure of the stand on stand-level characteristics or the individuals themselves. The model focus varies from the individual tree, a gap in the forest, or an entire stand (Shugart and West 1980, Shugart 1984). The scale of application ranges from individual trees, to a small gap in the forest, to regional global change effects on species composition. This class of models, which consists of several hundred separate models, has been reviewed by many investigators and can be sub-divided in a number of useful ways. The most obvious dichotomy exists between empirical models and process-based models. At one end of the continuum are models based on many regression variables and which fit the data quite well. At the other end are models which attempt to includes much current knowledge as possible concerning the actual biological processes involved. In reality, different parts of individual models fall along different parts of this continuum. For instance, a model may handle one form of competition (e.g. light) in a physically accurate manner and then include a term for horizontal competition (which represents competition for soil moisture and nutrients) that is empirically-based. After a brief description of the former empirical models, I will focus on the latter, since these have greater potential for interaction with pest management models.

Empirical population models

The empirical models are used primarily to assess growth and yield and are based on large site-specific data sets collected over a period of years or decades. Regressions are then derived which describe the *past* growth of these stands. The results of a modeling run may be very accurate if the modeled stand and the calibration stand have similar site qualities. On the other hand, these models are difficult to use on new sites or under new climate, pollution, or management strategies since different climates and nutrient availabilities significantly affect production rates. Dale *et al.* (1985), in a review paper of "tree-growth models (analogous to this "population model" class), refer to these empirical tree-growth models as "forest growth" models. They point out that forest growth models can be derived from the output of process-based models, but not vice versa. FOREST is an important example in this class (Ek and Monserud 1974).

Another type of empirically-based population model, known as Markov chain models, predicts species composition based on a transitional probability matrix. The composition of a forest in a future year or decade is assumed to be dependent only upon the current composition of the forest. (If past states are important, this is considered a higher-order Markov process.) Markov chain models of forest succession were first introduced by Waggoner and Stephens (1970), who predicted the likelihood of changes in forest cover type each decade based only on the current forest cover type. Horn (1975) expanded this concept to create a tree-by-tree transitional probability matrix. He also noted that forests tend to move toward a climax independent of their initial species compositions. Thus forest succession usually fits the definition of a "regular Markov chain" wherein the transitional probability matrix forces the outcome of the model to tend toward climax (perhaps followed by disturbance and another inexorable march towards climax). Due to the mathematics involved, massive data sets are generally necessary to successfully parameterize these models (Shugart 1984).

Process-based population models

The process-based models, which Dale *et al.* (1985) refer to as "community dynamics models," are often developed with improvement of our understanding of an aspect of forest dynamics as the goal. They generally have species-specific data requirements and less extensive site-specific data requirements, making them easier to apply to new regions. Since the goal is to provide a sense of how a *typical* stand will react to various prescriptions or climate scenarios, the models tend to provide results which are less precise than the empirical models given a large site-specific calibration set. However, the process-based population models are appropriate for use over broader regions.

The process-based models each use some method of modifying the gross production of a given species by subtracting respiration losses. Three methods of considering this loss are common (Dale *et al.* 1985). The first is based upon the differences between the anabolic and catabolic metabolism rates. Since the anabolic (constructive) rate is related to the surface area and the catabolic (destructive) rate is based upon volume, the ratio of the two can be used to predict the difference between the two (Von Bertalanffy 1951). In even-aged stands, allometry can be used to estimate these metabolic rates and therefore net production (Pienaar and Turnbull 1973). The second method uses non-multiplicative limitations on growth. In other words; climate variability, shading, nutrient competition, and soil moisture are explicitly modeled but act by Leibig's law of the minimum. The third method considers limitations on growth to be directly multiplicative. Potential growth of a tree grown alone (out in the open) may be reduced by an age factor multiplied by a shading factor multiplied by a water limitation and so on to include a temperature, nutrient, and other limitations.

Competition among individual trees may be modeled in many ways. These include distance-independent stand density measures, influence-zone overlap indices, distance-weighted size ratios, growing space polygons, mean distance to an arbitrary number of neighbors, distance to nearest neighbor and others (Adlard 1974, Munro 1974, Dale *et al.* 1985). Stand density measures are based upon basal area, or as in the case of JABOWA, on basal area and maximum expected basal area (Botkin *et al.* 1972). The advantage of this method is that it does not require detailed stem maps which are generally only available on intensively studied permanent plots. The disadvantage is that little can be learned about the reaction of an individual tree to a treatment or natural disturbance (e.g. pest infestation).

Influence-zone overlap indices are based on a circular zone around each individual tree with the radius of the circle based on a measure or measures of tree size such as dbh, crown radius, rooting radius, or height. The overlap of zones provides an estimation of the severity of crowding, which can then be used to decrement the potential dbh increase. This is an improvement over earlier methods which simply counted how many circles overlapped with the tree in question.

Distance-weighted size ratios use the product of the distance to a competitor and the relative size of that competitor. Hegyi (1974) was the first to use this method. Later, a cross between the influence-zone overlap method and the distance-weighted method was developed which accounted for more intense competition at the points of greatest overlap (Monserud and Ek 1977).

Using growing space polygons is another sophisticated method of modeling competition. Polygons are calculated among all of the stems in the stand, with the distance from stem to polygon

edge being determined by the distance to the nearest neighbor in a given direction and the relative sizes of the two stems. This is described in detail by Adlard (1974).

Other methods of characterizing competition exist as well, but are not as widespread as those described above. It is worth noting that while the above methods of describing competition attempt to be biophysical in nature, they are somewhat arbitrary and based generally upon the modelers intuition of what characteristics are important to include in the algorithm. They usually assume above-ground and below-ground processes, as well as light competition, which is a vertical biomass distribution issue, can all be described by a horizontal stem chart. They are still significantly more process-oriented than the regression-based models.

Ecosystem/Tissue Models

The defining characteristic of ecosystem/tissue models is that they tend to lump all green biomass into one category, thus eliminating much of the biochemistry that is explicitly modeled in the physiology-based models. Most of them do not model individual trees on a tree list as the population models do, either. The objectives of these models vary considerably, but they tend to involve the ecosystem-level effects of various management prescriptions, natural disturbances, or climate change. They typically include a carbon-based "currency" which is monitored as it flows from compartment to compartment. A major distinction can be made between those ecosystem/tissue models which include nutrient cycles in addition to carbon (primarily nitrogen and sometimes phosphorous or sulfur) and those which do not. The former were determined to be significantly more useful by Pastor and Post (1985, 1986), thus most models currently being used or developed now include at least a nitrogen cycle of some sort in addition to the carbon cycle. Some of the models consider varying levels of recalcitrance in the carbon compounds as well (e.g. starch, cellulose, lignin, humus). These more sophisticated models are capable of considering relative changes in production and decomposition changes explicitly, which is important in modeling global change scenarios since production and decomposition may decouple. Examples of this class of models include CENTURY-*forest*, MBL-GEM, PnET-CN, and Q.

The descriptions of production and decomposition in ecosystem/ tissue models vary from the nearly the same level of detail as some of the physiology-based models to much simpler (Ryan *et al.* 1995a). A direct calculation of gross photosynthesis minus respiration to determine net production available for allocation is the more sophisticated method. Nutrient to productivity and light to productivity ratios are used in other models to estimate directly the net production. The level of sophistication in the decomposition aspects of a model is constrained by the number of pools used to describe litter and soil. A sophisticated soil organic submodel of CENTURY includes structural

(recalcitrant, such as lignin) and metabolic (labile) carbon, nitrogen, and phosphorous components in no less than nine pools (surface litter, root litter, surface microbial, active soil organic matter, slow soil organic matter, passive soil organic matter, mineralized, leached organic, and leached inorganic). This allows detailed modeling of fertility effects of various disturbances or climate change. A model such as this could be used to compare the labile nutrient pools immediately after a pest defoliation event, considering that the decomposition of pests and pest by-products may be different than a natural litterfall event. A defoliation event would also change the microenvironment for re-invading species. A root pest would likely have effects on labile soil nutrients as well. Simpler models lump all of the soil organic matter pools into one, and do not differentiate differing qualities of litterfall. These models will often give different results than those which focus on soil processes.

Regional and Global Models

This class of models can be divided between those which strictly focus on ecological processes and those which include sociological and econometric phenomena. An argument could be made that the latter should not be included in this document, but they will be addressed briefly due to the potential for integrating them with pest management models. Those that are based on ecological processes can be further sub-divided into those which seek to model ecological processes primarily for the study of ecology, and those which are used to provide a surface parameterization for atmospheric models. Again, this latter class may not appear germane, but the inclusion of simple (and sophisticated) vegetation models in general circulation models and mesoscale weather forecasting models is currently a topic of intense discussion.

Ecology-based regional and global models

Regional and global ecology models produced primarily for the study of ecology are of several types. One type consists of those that take advantage of the well recognized correlation between climate patterns and biome distributions. As noted by Ågren (1991), initially these were based on the Holdridge Life Zone Classification System (Holdridge 1947, 1964), simply overlaying climate and vegetation maps. More recent attempts have correlated climatic variables such as precipitation, potential evapotranspiration, actual evapotranspiration, and others with the biome types (see, for example Emanuel 1985a, 1985b). Another approach is to predict net primary productivity, litterfall, and/or decomposition patterns across a continent or the globe (Rosenzweig 1968, Meentemeyer *et al.* 1978). Finally, some of the physiology-based and ecosystem/tissue models have been used with regional databases in a Geographical Information System (GIS) to determine region-wide reactions of ecosystems to climate change or fumigation with pollution (see Burke *et al.* 1991, for an example using CENTURY). Another example is a quantitative model comparison of

BIOME-BGC, CENTURY, and TEM. This study is using climate data input on a 0.5° x 0.5° grid for the entire lower 48 United States to compare predicted current potential vegetation maps and predicted potential vegetation maps given a 2 x CO_2 scenario (VEMAP Participants 1995). This question of how to scale up from leaf to globe is an important question for many modelers today (Ehleringer and Field 1993). There is no reason that region-wide patterns of pest infestation should be excluded from this discussion.

Using ecological models to provide a surface parameterization for climate or weather models is a recent phenomenon. Pielke *et al.* (1993) showed that a small decrease in surface albedo can result in an increase of equilibrium atmospheric temperature as large as the hypothesized "greenhouse" effect. On a landscape scale, Pielke and Avissar (1990) showed that an area of unstressed forest adjacent to a denuded area can cause winds as intense as a sea breeze, suggesting that large changes in leaf area from a pest could conceivably result in local weather changes. These regional or smaller-application models have greater potential for interaction with pest models, though admittedly even that interaction is unlikely to be significant. Most of these models strive to determine leaf area, transpiration rates, carbon and other trace gas fluxes, surface roughness, and/or albedo which can all be valuable inputs for atmospheric models. Typically, only an equilibrium solution for ecosystem effects on the atmosphere are sought, however a two-way interaction with dynamic feedbacks between ecosystems and the atmosphere are under development (Pielke et al. 1993). This development would make this class of models more useful to pest management modelers. Apparently, agricultural futures traders are interested in this latest development in weather forecasting (Schimel, *pers. comm.*). Examples of these equilibrium solution models are LEAF, BATS, and SIB.

Integrated socioeconomic-ecological regional models

Fully integrated models which include sociology, economics, and ecology have greater potential for interaction with pest management models since economics enter into the cost-benefit analysis associated with pest management. An argument has been made that forests serve as critical foci for integrated regional analyses for a variety of reasons (Pickett *et al.* 1994). Those authors also suggest that sociology and economics determine land use patterns, which in turn affect natural disturbance regimes including disease. Often, models in this class incorporate aspects of many other classes of models such as scenic quality, population, and econometric models. These models have been divided into three types; inventory/descriptive, engineering/optimization, statistical/econometric (Parks 1992).

The inventory/descriptive integrated regional models typically include economics implicitly rather than explicitly. Current and historic land use data are collected and then used to develop trends. The mathematics of these trends may be expressed deterministically or stochastically, perhaps using a Markov chain process. The land use trends may then be correlated with economic and political development of a region or directly with ecologically significant phenomena. An example of the latter is a study examining carbon flux from the Soviet Union between 1850 and 1980, a period of rapid development including decades of rapid deforestation (Melillo *et al.* 1988).

Engineering/optimization regional models strive to maximize certain quantities within other constraints. This is the type of model currently used for National Forest planning. (See for example USDA Forest Service 1987a, 1987b.) Pest management can be integrated into these models successfully. Since these models are used so widely within the Forest Service, they will not be discussed further here.

Statistical/econometric regional models take a slightly different approach wherein the economic, social, environmental policies and are taken as the input. The land use is then determined, not as an optimal plan developed by the model, but rather as likely outcomes determined empirically. This method allows economic considerations to be explicitly incorporated into a landscape model rather than incorporating a landscape model into an econometric optimization model. See Turner (1987 and 1988) for an example of a statistical/econometric model successfully incorporated into a spatial landscape model.

Model Examples

The intent of these summaries is to review the development of the models, summarize the primary simulation processes, and present a few of their applications. This will provide a detailed example from each class of models. Since the most current versions of these model cannot be adequately discussed in isolation, a brief recap of their history will be presented in conjunction with issues of scale across time and space. This will be followed by a summary of the key processes and variables. Finally, applications and the future of the models will be discussed.

BIOME-BGC (BioGeochemical Cycling)

History and scaling issues

BIOME-BGC is the latest in a series of physiology-based models which have demonstrated impressive longevity. Though it is now being used to map global net primary production (NPP) and

nitrogen cycling over a period of centuries, dates back to the mid-1970's when its precursor, H2OTRANS (Running *et al.* 1975, Waring and Running 1976), simulated the water budget of a single tree over a period of days. Originally, Waring and Running noted that stomates of *Pseudotsuga menziesii* (Douglas-fir) closed at 30 mbar and they wanted to investigate the effects of this finding on the hydrologic budget of a single tree and, later, an entire stand. DAYTRANS (Running 1984a) was the first attempt to take these hourly water status estimates and scale them up in time. The internal flow dynamics were simplified in the development of DAYTRANS as Running and others worked to create an average daily water budget. The first step toward including productivity estimates was embodied in DAYTRANS/PSN (Running 1984b), which added a canopy photosynthesis subroutine. Of course, the rest of the carbon budget was absent in these early, single tree models. The first version of FOREST-BGC (Running and Coughlan 1988) added respiration, within-tree carbon allocation, litterfall, and decomposition. Other critical developments at this stage included scaling up across space to encompass a 1-ha stand. At this stage, horizontal homogeneity was assumed and only vertical fluxes of H_2O and C were considered. A dual timestep was instituted to accommodate scale issues such as the difference in the rates of soil water uptake and carbon allocation. The former was iterated daily and the latter annually. The essential components of this model have remained unchanged and those that remain in BIOME-BGC are discussed in detail below.

A later version of FOREST-BGC (Running and Gower 1991) added a nitrogen cycle, explicitly connected to the carbon cycle discussed above. The dual timestep remained, but was made more flexible to allow investigations of high frequency variations in hydrology (e.g. hourly) and intra-season variability in NPP. The primary change in developing BIOME-BGC (Running and Hunt 1993) was the addition of multiple vegetation types and climate scenarios. BIOME-BGC and the most recent version of FOREST-BGC will be the focus of the process summaries below.

Model philosophy

A key goal of the BGC family of models is a design which allows the use of remotely sensed and other easily accessible data (Running and Coughlan 1988). For instance, leaf area index (LAI) is an important driving variable in many processes either directly, such as for canopy interception, canopy evaporation, transpiration, canopy light attenuation, photosynthesis and canopy nitrogen content (Running *et al.* 1989), or indirectly by affecting soil temperature and moisture, for example nitrogen mineralization and heterotrophic respiration (Hunt 1993a). An estimate of LAI can be derived from remote sensing data (Running *et al.* 1986, Ford *et al.* 1994) from coarse resolution platforms such as the Advanced Very High Resolution Radiometer (AVHRR, 1.1 X 1.1 km) or fine resolution platforms such as the Thematic Mapper (30 X 30m). The most common proxy for LAI

is the Normalized Difference Vegetation Index (NDVI) which is a derivation of the difference between infrared and red reflectance, providing an estimate of the absorbed photosynthetically active radiation (APAR). Running *et al.* (1986) provide support for the LAI/NDVI correlation. However, Running and Hunt (1993) do not explicitly recommend an algorithm for estimating LAI for other biomes which have different areal extent of bare soil. Running (1990) acknowledges that this is an important issue, however.

Another example of easily obtained driving variables is NOAA climate data. The three dimensional versions of the model (e.g. Regional Hydro-Ecological Simulation System (RHESSys), discussed below) use a mountain microclimate model (MT-CLIM) to estimate climatology between meteorological stations (Running *et al.* 1987). This submodel uses elevation, slope, aspect, east-west horizon angles, LAI, as well as maximum and minimum air temperature, dewpoint, and precipitation data from regional meteorological stations. Four subroutines then calculate site-specific values of incoming short-wave radiation, air temperature, humidity and vapor pressure deficit, and precipitation. Running *et al.* (1987) admit that the results are somewhat unsatisfactory due to simplifications (e.g. no inversions, cold air drainage, wind) and the paucity of meteorological stations covering the planet. Incidentally, BIOME-BGC uses MT-CLIM2, which incorporates unspecified modifications to the older version (Hunt 1993a). In any case, the use of remotely sensed and meteorological data allow the model to be scaled across regions and the globe easily.

Finally, the models use a self-proclaimed "minimalist philosophy" (Running and Hunt 1993) wherein additional subroutines and variables are only added if deemed necessary. This was an important criterion during the generalization of FOREST-BGC to BIOME-BGC. For instance, rather than entirely revamping FOREST-BGC, many physiological processes are assumed to be universal, such as stomatal control by APAR, air temperature, vapor pressure deficit, and soil water potential.

The primary change was the addition of "leaf ON" and "leaf OFF" dates for seven biome numbers. Though published information on BIOME-BGC (Running and Hunt 1993) discusses only three biomes, the User Guide (Hunt 1993b) clearly delineates seven possibilities as follows: 1) conifer, leaves always "ON", fine root compartment status determined by the soil water and temperature, 2) deciduous forest, leaf off and on dates defined by the user, 3) shrubs, leaf off and on dates defined by user, 4) grassland, leaves and fine roots determined by soil water and temperature status, 5) agriculture, dates defined by user, 6) tropical evergreen broadleaf, leaves and fine roots always on, and 7) other, dates defined by the user. Effectively, there are many times this number of biome types represented, since a variety of climates are associated with the above functional types. For

example, temperate rainforest in the Pacific Northwest and a lodgepole forest in Colorado may be differentiated solely by climate (and LAI). Other important parameters that vary among biomes include specific leaf area; maximum stomatal conductance and photosynthetic rates; respiration rates and turnover rates of leaf, stem, and root compartments; critical leaf water potential; and leaf lignin concentration.

Process summaries

The process summaries will be discussed in order of importance in BIOME-BGC, which coincides with the length of their history in model development. In other words, the hydrologic budget appears first (Running *et al.* 1975), then a carbon budget (Running and Coughlan 1988), followed by a nitrogen budget (Running and Gower 1991). The following summary relies heavily upon Hunt (1993a).

Clearly, the hydrologic cycle dominates this family of models. Output from MT-CLIM2, in conjunction with LAI (set to zero if leaves are off), is used to calculate APAR (including calculation of day length), average daily temperature (actually just the average of daily extremes), vapor pressure deficit, radiation absorbed (using Beer's Law), and soil temperature (based upon the previous day's value plus a fraction of the current day's transmitted radiation). Water is divided into snow or rain based upon the average nighttime temperature. Snow does not accumulate in the canopy, but goes directly onto the snowpack, which then melts according to ambient temperature and incident radiation. Initially, a fraction of rain (proportional to LAI) is intercepted in the canopy to be evaporated at a rate limited by radiation and air temperature. Throughfall is routed to soil water compartment and infiltration rates are not limited (!). BIOME-BGC currently uses maximum volumetric water content, but ultimately will allow explicit soil texture treatment. Excess precipitation is runoff, not considered further in BIOME-BGC, but is critical to regional models such as RHESSys (Running *et al.* 1989). Direct evaporation is determined using a modified Penman-Montieth equation. Remaining soil water and soil texture are used to determine the soil water potential. If this potential is above that necessary to prevent stomatal closure, stomatal conductance is calculated as a function of LAI and the slope of stomatal conductance per light intensity. From this, the water cycle can be closed by estimating transpiration. At this stage, the proportion of C_3 versus C_4 plants is used to determine a total canopy stomatal conductance. This value is modified by a boundary layer conductance. Finally, the same modified Penman-Monteith equation used for soil surface evaporation is used to determine the transpiration rate.

Since a carbon cycle was first implemented with FOREST-BGC, not all components of the cycle are treated in as much detail as the hydrologic budget (Ryan *et al.* in press (a)). BIOME-BGC

treats the physiology of canopy gas exchange in more detail than previous versions, however (Hunt and Running 1992). The photosynthesis rate follows an inverse parabolic function based on measured maximum and optimum photosynthetic rates, separable by C_3/C_4 pathways. An average total canopy light use efficiency accounts for the proportion of each pathway present in the ecosystem. Total canopy photosynthesis is modified by LAI, CO_2 concentration, air temperature based on a Q_{10} of 2.0, and Rubisco limitation (providing a critical linkage to the nitrogen cycle). Growth is simultaneously limited by water potential, photosynthesis, and nitrogen availability, with the greatest limitation governing.

Growth respiration is proportional to the growth allocation, iterated annually. Maintenance respiration is iterated daily. Since photosynthesis includes daytime maintenance respiration for the leaves, this only needs to be calculated for nighttime. Nighttime leaf maintenance respiration, as well as 24 hr stem and coarse root respiration are based on exponential functions of average and extreme temperature, again with Q_{10} set to 2.0.

The nitrogen cycle is inextricable from the carbon cycle for certain portions of the model, thus they will be considered simultaneously henceforth. Note that nitrogen allocations are all made on an annual timestep while some carbon allocations (photosynthesis and maintenance respiration) are made daily. In addition to being a critical limiting factor to leaf growth, the role of nitrogen in litter and fine root biomass decomposition is explicitly simulated. Litter respiration simulation first combines the fine root biomass and litter biomass compartments. Maximum litter respiration rates are from the literature. Lignin concentrations of litter are calculated based upon leaf nitrogen values, allocated annually, and assuming that fine root lignin is half that of leaves. Nitrogen retranslocation prior to leaf abscission is considered, but fine root nitrogen is assumed to be lost to the soil nitrogen pool. Total litter respiration and nitrogen mineralization are then calculated based upon the lignin to nitrogen ratio, carbon content of litter, soil water and soil temperature.

In summary, a remotely sensed LAI proxy and meteorology data drive the daily water cycle. Daily carbon budgets, APAR and evapotranspiration are transferred to the annual portion of the model. Carbon and nitrogen are annually allocated to leaf, stem, coarse root, fine root, litter, and soil compartments. The first four of these values are returned to the daily timestep portion of the model.

Applications and prospects for the future

The applications of FOREST-BGC and BIOME-BGC have grown with the model. Initially, the intent was to model water, then carbon and nitrogen flows in the vertical dimension only. The advent of the Regional Ecological Simulation System (RESSys) allowed topography and soil type to

vary across a region (Running *et al.* 1989). A more recent version (RHESSys) explicitly simulates water flow across the landscape (Band *et al.* 1991). Ultimately, RHESSys-GCM will be produced with a shorter timestep which can interface with the Biosphere-Atmosphere Transfer Scheme model (Running and Hunt 1993). Another important application of the model is simulation of productivity across regions (Hunt and Running 1992) and the globe (Running and Hunt 1993). This includes the VEMAP project which involves several researchers at Colorado State University. Many of these applications assess effects of a doubling of CO_2 on temperate coniferous forests (Running and Nemani 1991, Ryan *et al.* in press (b)). In addition, many researchers use the model to augment their field work. For instance, a dendrochronology study of alpine treeline (Scuderi *et al.* 1993) uses FOREST-BGC. A physiology-based model such as this has great potential to interface with pest management models. For instance, defoliators have a direct and immediate effect on LAI, which is easily manipulated in BIOME-BGC. Root diseases would affect nutrient uptake in ways that could also be simulated using the model. Finally, the output of BIOME-BGC includes LAI and nitrogen concentration in the leaves, which could be used to help predict patterns of pest outbreak.

A.D. Friend has developed a bridge, called HYBRID (Friend *et al.* 1993), which communicates with a gap model to include succession and transient effects of global change. Individual trees fix, respire, and allocate carbon, as well as transpire. The growth equation in ZELIG, a population model, are replaced with more realistic process-based functions, allowing HYBRID to include processes in competition and physiology.

The Earth Observing System, scheduled for launch in June of 1998 will carry an enhanced set of sensing devices with better spatial and spectral resolution than the AVHRR satellites. Algorithms for vegetation classification are being improved and plans are being made to interface this new, remotely sensed data set with BIOME-BGC (Running *et al.* 1994). Ultimately, the developers of this family of models envision a modular system of ecological models which will be available to researchers via modem, wherein the individual can choose the scale of the simulation with which s/he wishes to work (Ford *et al.* 1994).

JABOWA/FORET (JAnak, BOtkin, and WAllis)

History and Scaling Issues

In 1972, Botkin and others published the first population-based model, JABOWA (Botkin *et al.* 1972a, 1972b), which was later modified to become FORET (Shugart and West 1977), spawning an entire generation of forest simulation models. The latter is of particular interest, because it was

developed to simulate the effects of a pest, *Endothia parasitica* (the organism that caused chestnut blight), on species composition and basal area in the East. These models strive to simulate the birth, growth, and death of every tree on a circular plot. Initially, this plot size was 1/100 of a hectare, and in FORET was increased to 1/12 ha. JABOWA was developed with data collected at the Hubbard Brook Forest where information on elevation, aspect, slope, percentage of the plot in rock, till depth, and soil moisture were available. One of the original goals was to make the model general enough that parameterization of the model could be completed with minimal additional field work. Thus, the model originally applied to only the 13 species of hardwoods present on the plots. Species-specific input includes a maximum observed age, maximum diameter, maximum height, a height-diameter relationship, a total leaf weight-diameter relationship, a light intensity dependent photosynthesis rate, a climate dependent growth rate, a required soil moisture range, and a sapling germination rate based on shading. Abiotic input variables include elevation, soil depth, field capacity of the soil, percentage rock in the soil profile, average monthly temperature and precipitation, and an annual insolation value. JABOWA's computer code can be divide into three primary subroutines; GROW, BIRTH, and KILL. The authors of FORET added GAUSS and SPROUT, to refine meteorological input and to reflect vegetative reproduction on their Anderson County, Tennessee site. After initializing the stand, the subroutines are called in the following order; GAUSS, BIRTH, SPROUT, KILL, and GROW (see flowcharts in Appendix B). Each of these subroutines is discussed below.

Process summaries

The effect of temperature on photosynthetic rates is not as detailed as the daily consideration of soil and air temperature in BIOME-BGC, but an attempt is made to include the effect in a general way. A parabolic function was described on the basis of growing degree-days per year. Growing degree-days are defined as the product of the number of days above a certain temperature and the number of degrees above the threshold temperature (40°F in JABOWA and 42°F in FORET). The parabola is defined to equal zero at the minimum and maximum number of growing degree-days for each species. These extremes are defined by comparing range maps of each species with January and July isotherms on a global map. The parabola is considered to be symmetrical, with a maximum of 1 reached at the apex. The fraction between 0 and 1 is then used in the reproductive (BIRTH) and growth (GROW) subroutines. This is an example of modeling a process in a way that is not at either extreme of the process-based/empirical continuum. The subroutine GAUSS, added in FORET, is simply a way of including temperature variability from year to year. A random-number generator is used to choose a growing degree-day value which reflects the mean and variance of the climate in Anderson County, Tennessee, where the model was validated.

The BIRTH subroutine reflects sexual reproduction in a way that includes species-specific probabilities of germination based on shade tolerance, growing degree-day and soil moisture conditions, as well as a stochastic element. In the JABOWA version of BIRTH, the first determination is whether a given species of tree could grow given the climatology of the plot. If a species can, it is available to be "planted" on the plot. Of the available species, one is selected randomly (which assumes that a seed source is available for each of the species) and zero, one, or two saplings are planted on the plot. Their diameter is greater than 0.5 cm by a small, random increment. However, a different process holds for those species which depend strongly on successional conditions (the two birch and two cherry species). If the leaf area of the plot is below a certain threshold (CHERRY), the light conditions are considered to be adequate for the germination of sixty to seventy-five new cherry trees of one of the species. This density is actually far below that observed at Hubbard Brook. Rather than increase the computational requirements of the program unnecessarily, the authors felt it was reasonable to start with too few added cherries, but then gave them a higher probability of survival in the KILL subroutine. This results in a realistic number of cherry stems 10 years after a clearcut. If the leaf area is above CHERRY, but below a second threshold, BIRCH, then 0 to 13 new birches are added to the plot, with the number selection weighted in such a way that fewer enter the plot as the leaf area approaches BIRCH.

The BIRTH subroutine in FORET is more sophisticated. Four questions are addressed in relation to each of 33 species-specific requirements. First, how much mineral soil is available? And second, how much is there leaf litter on the soil? These two can be determined by calculating LAI. Third, is the year hotter than average? This is determined using GAUSS. And finally, is it a year of small mammal or deer abundance? Incidentally, this question seems easily adapted to pest infestation probability. These four questions are used as tests to determine which species are eligible for reproduction. The model then selects 0 to 7 individual of 1 to 3 species of trees to plant. They enter the plot at a random size tightly clustered about a mean of 1.27 cm dbh. Six old-field successional species represent an exception to the above discussion. These are only capable of reproduction if a seed tree of the same species has been available on the plot in the past 20 or 30 years (species-specific). In effect, this is a Markovian process but with information on germination requirements built into the transitional probability matrix.

The subroutine SPROUT was developed by Shugart and West to include the vegetative reproduction common in southeastern forests. If a tree is killed in the KILL subroutine, then two questions are asked. First, is the species one that typically reproduces by sprouting from stumps or roots? If the answer is yes, then the question is asked if the dead tree was of the proper diameter to sprout (e.g. between 12 cm and 200 cm for *Acer saccharum* or between 6cm and 20 cm for *Fagus gran-*

difolia). If the answer is again yes, then one, two, or three sprouts are added to the plot (e.g. 3 if *A. saccharum*, 2 if *F. grandifolia*). These small samplings are then treated as any other tree on the plot.

The KILL subroutine is run before the GROW subroutine to save computations on trees that are about to die anyhow. The subroutines, the same in JABOWA and FORET, assume that death is an age-independent stochastic event. A maximum observed age (AGEMX) is entered and only 2% of saplings which continue to actively grow are expected to reach maximum age. The probability that a given tree that is actively growing will die in a given year is approximately 4/AGEMX (e.g. 4/300 yrs = 1.3%/yr for *A. saccharum*, 4/400 yrs = 1.0%/yr for *F. grandifolia)*. In addition, if the growth rate of a tree falls below 0.01 cm/yr then the probability of surviving 10 years is assumed to be 1%. This implies a probability of dying equal to 36.8% in any given year for trees which are no longer actively growing. This empirical treatment of death ignores the subtleties of death due to varying causes such as blowdowns, lightning, parasitism, or defoliation, the authors readily admit. This appears to be an area of potential improvement which could explicitly include the probability of death due to pest infestations of various types.

The GROW subroutine is the heart of this type of model. The growth rate equation takes the form of:

$$\frac{d[D^2H]}{dt} = RLA\left(1 - \frac{DH}{D_{max}H_{max}}\right)(shading)\ (climate)\ (crowding)\ (soil)$$

where: D= diameter,
H = height,
R = growth rate parameter,
LA = Leaf Area of the tree,
D_{max} = maximum recorded dbh, and
H_{max} = maximum recorded height
and shading, climate, crowding, and soil are reductions in the growth rate ranging from 0 to 1 as discussed below.

Since DH approaches $D_{max}H_{max}$ as time goes on, the growth increment decreases forcing the optimal growth curve to a sigmoid function. This is an implicit treatment of increased woody respiration or other explanations of decreased growth in older trees. The above annual growth increment is for the optimal case wherein shading, crowding, and sub-optimal climate are absent. When any of these are present, the optimal growth increment is decreased as described below.

Shading is calculated as a function of the leaf area of all trees that are taller than a given tree in the plot. Tree heights are estimated with an empirical function based on the diameter. Light extinction is then calculated based on the leaf area above a given tree and the incident radiation at the top of the canopy. The reduction in growth is species-specific, such that shade-tolerant species are affected the least. Each of the growth-limiting factors is scaled such that the factor is equal to 1 if there is no limitation due to the factor (shade in this case) and 0 if the limitation is complete. This fraction is then multiplied by the optimal growth increment calculated in the above growth equation.

The effect of sub-optimal climate on growth is fitted to a parabolic function, as described above. The function equals 1 at optimal temperatures and 0 at the extremes of the species climate range. This fraction is then multiplied into the growth equation. A later version includes frost-tolerance as a climate variable (Solomon *et al.* 1984). Competition for nutrients is considered implicitly by creating a competition index. This factor is equal to 1 when the plot is devoid of trees and is equal to 0 when the basal area is equal to the maximum basal area of the plot under optimal growing conditions. In between, the effect of crowding is linear. (In other words, if basal area is 0.75 of the maximum, this factor will be equal to 0.25.) Like the above, this factor decreases the growth increment by multiplying it into the growth equation. In JABOWA, This crowding index accounts only for nutrient competition. Water availability is modeled more explicitly, taking into account precipitation, soil depth, soil water-holding capacity based on texture, and percentage of rock fragments. In the case of FORET, the crowding index takes into account nutrient and water competition. Shugart and West (1977) eliminated the soil water subroutine, stating that on their low-slope position plots, water is never limiting.

Applications and prospects for the future

The models have been used for a variety of purposes. The initial validations were for the Hubbard Brook Forest (JABOWA) and pre-chestnut blight and post-blight conditions in Anderson County, Tennessee. Other applications include the prediction of chronic air pollution on southeaster U.S., investigation of a Quaternary pollen chronology (Solomon *et al.* 1980), prediction of bird habitat after selective hardwood harvest (Smith *et al.* 1981), and an investigation of hysteresis in theoretical two-species forests under warming and cooling climates (Shugart *et al.* 1981).

Many modelers refer to the JABOWA/FORET class of models, meaning population models which simulate mixed-species, mixed-age stands by tracking the birth, growth, and death of individuals. Many models have their conceptual roots in the original JABOWA and FORET efforts. These in turn have had many applications such as predicting the effects of different management regimes

on growth and yield in northern hardwood forests (FORTNITE, Aber *et al.* 1982), nutrient retention in forests (Weinstein *et al.* 1982), transient effects of climate change (FORENA, Solomon 1986), and integrated investigations of the role of species, soil moisture and climate, on carbon and nitrogen cycles (LINKAGES, Pastor and Post 1986, 1987, 1988). The Pastor and Post models simulate decomposition using lignin to nitrogen ratios. The trend is towards more process-based subroutines in the more modern population models. The most recent innovations in this class have been models like HYBRID and LINKAGES which seek to link the physiology-based models with population based models.

CENTURY-forest

History and scaling issues

The CENTURY-*forest* model developed from the original CENTURY grassland model which had been in existence for nearly a decade before the new version was developed. CENTURY is an example of an ecosystem/tissue model which does not differentiate individual plants, but rather lumps them into a few compartments. The strength of the CENTURY models is the soil organic matter submodel which separates soil into several pools with varying turnover times. For instance in the original grassland model, soil carbon is split into active soil carbon (1.5 yrs.), slow soil carbon (25 yrs.), passive soil (1000 yrs.) (Parton *et al.* 1987). This allows investigations into long-term and short-term changes in soil carbon. Nitrogen was also simulated with the same number of pools. A later version added phosphorous and sulfur submodels with analogous pools, in addition to pools to account for differences in the soil chemistries of those elements (Parton *et al.* 1988). For example, occluded phosphorous and atmospheric deposition of sulfur were added. The first attempt to add trees to the model simply adjusted the rates of processes, elemental ratios and so on, without adding any new compartments to the model (Parton et al. 1989). A significant advance was made when woody tissues were given their own compartments, as described by Sanford *et al.* (1991). These will be discussed in detail below. The model has also been used to simulate savanna and crop systems.

The time step of the model is currently one month, though it can easily be adapted to run on a shorter time step. The spatial scale of simulation is not explicit. It is essentially a one dimensional model with flows occurring up into plants or down into the soil subcompartments. This does not preclude the model from being applied to entire forest stands or even regions. For example Burke *et al.* (1991) applied the model to grid cells across the Great Plains to simulate soil organic matter dynamics across the region. Input and output are reported in grams per square meter and can be scaled to any size of interest. The major required input variables include monthly average and ex-

treme temperatures; monthly precipitation; plant carbon, nitrogen, lignin, phosphorous, and sulfur contents; soil texture and pH; atmospheric and soil nitrogen inputs; and initial carbon, nitrogen, phosphorous, and sulfur contents of the soil. The phosphorous and sulfur portions of simulations may be omitted if they are not desired.

Process summaries

The processes simulated by the CENTURY family of models can be sub-divided into the soil organic submodel; a water budget and soil temperature submodel; nitrogen, phosphorous, and sulfur submodels; and plant production submodels for grass, crop, forest, and savanna. We will focus on the forest submodel in this summary. This summary is primarily based on information available in the User's Guide to CENTURY (Parton *et al.* 1992). More detailed information is available in other publications which occasionally appears contradictory (e.g. Parton *et al.* 1987, 1988). These discrepancies are a sign that the model is successful and has survived a series of adaptations. The authors have shared their model widely, which lead to many variations as well as applications of the model.

The soil organic matter (SOM) submodel consists of nine pools; structural and metabolic carbon in above- and below-ground litter, surface and subsurface microbial pools, slow SOM, passive SOM, and leached carbon. See the flowcharts in Appendix B. Breaking the decomposition process into this many pools allows detailed analysis of long term SOM dynamics. Flows among the pools are controlled by rates determined by various biotic and abiotic variables. For instance, how much plant litter is considered structural or metabolic depends upon the C:N and lignin:N ratios. Metabolic plant material, which contains no lignin, is assigned a much higher decomposition rate (i.e. it goes through the microbial pool) whereas the lignin goes directly to the slow SOM pool. The rate of turnover in the subsurface microbial pool is dependent upon soil texture but the surface microbial pool is not. Turnover rates in all of the SOM pools are dependent on temperature and moisture. Average monthly temperature and the ratio of stored water in the top 30 cm of the soil are used to determine how much an optimal decomposition rate should be decreased. The temperature curve is a non-linear representation of empirical data which rises slowly from 0.05 to 1 between 0°C and 35°C then drops precipitously to 0 at 45°C. The moisture curve rises from 0.25 to 1.0 along asymptotically as precipitation increases. The effect of fine-textured (clayey) soils is an increase in the rate of stabilization of SOM (i.e. more goes into slow and passive SOM pools). Leached soil carbon only occurs out of the top 30 cm of soil and only if precipitation exceeds evaporation to create runoff.

The water budget and soil temperature submodel uses incoming climate data to create soil microclimate data. If the air temperature is below 0°C when precipitation occurs, it is considered to be snow. Snow melt then occurs as a linear function of average air temperature. Potential evaporation rate is a function of minimum and maximum monthly temperatures. Evaporation (or sublimation) occurs from snowpack, precipitation intercepted in the canopy, and from the bare soil. Any remaining water is added to the soil water compartments. Water is added to the top layer (0 cm to 15 cm) and any water in excess of the field capacity is added to the next layer (15 cm to 30 cm). This "tipping-bucket" analogy continues into the deeper layers. Layers are 15 cm thick until 60 cm below the surface and 30 cm thick thereafter. The number of layers included in the model is an input variable. Further water loss from the soil occurs either as transpiration or leaching. The former is determined by plant production rates and the latter is a measure of water that reaches beyond the deepest specified soil layer. Incidentally, this leached water can travel at various assigned rates to recharge streams and can interact with other submodels to carry away nutrients such as nitrate. Soil temperature is a function of air temperature and canopy biomass.

The structures of the nitrogen, phosphorous, and sulfur submodels are similar to the soil organic matter submodel. For instance in the nitrogen submodel, the C:N ratio remains constant at 150 in the structural plant litter pools (surface and subsurface). Excess nitrogen will be in the plant metabolic litter pools. This in turn will determine how nitrogen-rich the surface and subsurface microbial pools are. The C:N ratios for microbial by products determines how much nitrogen is mineralized. This is calculated on a net basis, gross immobilization and mineralization are not explicitly modeled. On a broad basis, metabolic plant residue leads to greater net nitrogen mineralization and structural plant litter allows less mineralization. Nitrogen can be artificially added to the soil as atmospheric deposition, fertilization, or plant residues as well. In addition to leaching, nitrogen is removed via crop removal or gaseous losses. The latter is a topic of current research in the field and data is being actively incorporated into the model. The phosphorous submodel is analogous except for the split of the mineral pool into five; labile, sorbed, parent, secondary, and occluded phosphorous. This allows explicit consideration of tropical soils which present difficulty for models which include a simple or no phosphorous consideration (see TEM, below). The sulfur submodel is analogous to the phosphorous submodel, except for the exclusion of occluded or sorbed sulfur pools. Details of the latter two submodels are available in Parton *et al.* (1988).

The plant production submodels are similar to each other. The forest submodel is the most complex in terms of the number of compartments modeled. The crop model is similar to the grass model except that it includes an explicit pool for grain production. It also allows for harvest, remaining plant residue, fertilization, and the effect of plowing on decomposition rates. The savanna model

is essentially a combination of the grass and forest submodels. Grass growth is modeled using a shading index dependent on tree canopy cover and leaf biomass. Fire effects and nitrogen competition between the life forms is also considered.

The forest submodel divides the plant into ten parts as follows: 1) leaves, 2) fine branches less than 5 cm in diameter, 3) large wood, 4) fine roots less than 2 mm in diameter, and 5) coarse roots are each divided into live and dead portions. Maximum monthly production is calculated as a function of available moisture, temperature, and maintenance respiration. The moisture effect is determined by combining the currently available soil moisture with that month's precipitation, and then dividing it by the potential evapotranspiration. Slightly different, but linear relationships exists between this value and production for sandy and fine-textured soils. Contrast this with the dependence of BIOME-BGC on a detailed daily hydrology. The temperature effect is based on a Q_{10} equal to 2.3. Maintenance respiration is calculated for each compartment using modifications of the same equations used in BIOME-BGC (Running and Coughlan 1988).

The production remaining after respiration is subtracted (NPP) is then available to be allocated to the different plant compartments. Allocation to immature and mature trees can be differentiated, but differences among species in allocation as well as production are not explicitly included in the model. Deciduous and evergreen trees are treated the differently by simply increasing the live leaf senescence dramatically during one month for the deciduous trees. When plant parts die, the C:N and lignin:N ratios are calculated to determine how much of each plant compartment goes to each portion of the SOM submodel. Disturbance can be explicitly modeled, using a forest management routine. Parton et al. (1992) suggest that this can be used to simulate different silvicultural practices, fire, and windthrow. The fraction of live leaves lost can be specified, as can the fraction that reaches the forest floor and the nutrient content of those plant parts. This is an area where pest impacts could be directly entered into the model to simulate the effects on soil organic matter, production the following years, and so on.

Applications and prospects for the future

As mentioned previously, CENTURY was developed as grassland simulator, focusing on soil organic matter dynamics. It's applications tend to focus around these strengths. The initial publication relating to the model simulated steady-state soil organic matter and plant productivity for 24 sites on the Great Plains (Parton *et al.* 1987). they were particularly interested in the effects of soil texture on SOM dynamics and productivity. Form the results, they extrapolated productivity and decomposition rates for the entire central U.S. grasslands. This approach is an example of how the minimum default size of simulation (implicitly one meter) does not necessarily prevent a model

from being used on regional and, conceivably, global scales. As mentioned previously, Burke et al. (1991) utilized CENTURY in conjunction with a GIS to simulate the productivity and soil organic matter dynamics on a pixel by pixel (0.5° x 0.5°) basis. Other studies have investigated land use practices such as wheat/fallow systems, fertilization regimes, etc. on localized areas (Parton *et al.* 1988). These studies can separately simulate the effects of atmospheric sulfur and nitrogen deposition, or phosphorous and nitrogen fertilization. Trace gas production from grasslands has also been a focus of recent research (Schimel *et al.* 1990).

Forest applications of CENTURY are less numerous since this portion of the model has not been in existence as long. The first application of the model to forested systems was incidental to an investigation of the formation of tropical soils. Separate compartmentalization of forest biomass did not occur until a study investigating the effects of hurricanes on Luquillo Experimental Forest in Puerto Rico (Sanford et al. 1991). Massive defoliation events were predicted to lead to higher levels of equilibrium soil organic matter due to the higher nutrient content of mature as opposed to senescing leaves. This defoliation effect is one way that CENTURY could interface with pest management models. Another idea is to simulate the effect of varying levels of soil nutrient status in relation to root diseases. The savanna submodel would be useful to determine the reaction of understory plants to a defoliator. Large scale applications of CENTURY, such as VEMAP, are unlikely to use pest infestation probabilities as input because the scale of analysis is so small. However, the output of regional forest analyses may prove useful for pest management modelers.

TEM (Terrestrial Ecosystem Model)

History and scaling issues

The Terrestrial Ecosystem Model or TEM was created to predict major carbon and nitrogen fluxes and pool sizes across continents and the entire planet. The development of the continental-scale Water Balance Model (Vörösmarty 1989) made this possible. The model is process-based but the plant and soil pools are highly aggregated (i.e. there is only one of each). Only five state variables were initially included; carbon in living vegetation (C_v), organic carbon in detritus and soils (C_s), nitrogen in living vegetation (N_v), organic nitrogen in detritus and soils (N_s), and available, inorganic nitrogen in soils (N_{av}). The nitrogen in living vegetation was later subdivided into structural (N_{vs}) and labile (N_{vl}) pools (McGuire et al. 1993, Melillo et al. 1993). The model is based upon grid cells 0.5° x 0.5° in size. At the equator these are nearly square and approximately 3090 km^2 in size. No interaction among the cells is considered. The model is run to equilibrium for each of the grid cells, excluding ice, water, and wetlands. Since it is run to equilibrium, the results only pertain to mature, undisturbed vegetation, making consideration of transient effects of climate

change impossible. The modelers chose to ignore the complexities of wetland chemistry for the time-being. This eliminates 1,466 grid cells, leaving 56,090 terrestrial grid cells in a global simulation. The model is parameterized for eighteen different vegetation types ranging from polar desert/alpine tundra to tropical evergreen forest. This vegetation data is combined with soil moisture and texture, potential and actual evapotranspiration rates, insolation and cloudiness, precipitation and temperature, as well as the atmospheric carbon dioxide concentration as input for the model. Vegetation, five soil textures, elevation, temperature and precipitation are used in the Water Balance Model to produce the above climate data necessary for input into the TEM. A geographical information system is used to keep track of the parameterization and output for each grid cell. The time-step of the model is monthly. This allows analysis of seasonal variations of NPP, which is an improvement over previous global models. The mathematical expressions governing fluxes among the six state variables are based on observations of the processes in the field. These are discussed in detail below.

Process summaries

The first publication of the model contains an appendix which describes the model in detail (Raich *et al.* 1991). Monthly estimates of NPP are made for each grid cell based on the difference between simulated gross primary productivity (GPP) and plant respiration. GPP is a function of many variables: a maximum carbon assimilation rate under optimal conditions, incident photosynthetically active radiation, fractional leaf area, temperature, carbon dioxide concentration, water availability, and nitrogen availability each affect the GPP. Maintenance and construction respiration are both included.

The maximum carbon assimilation rate is vegetation specific and varies from 492 g/m^2/month in deserts and arid shrublands to 1,898 g/m^2/month in tropical savannas. Incident PAR is reported for the top of the canopy. GPP increases hyperbolically with increasing radiation. Fractional leaf area is the percentage of the maximum annual leaf area for that vegetation type that is present in the month being simulated. Initially the temperature effect was modeled as a parabolic function with a maximum of 1 reached at the optimal growing temperature and a minimum of 0 reached at minimum and maximum growing temperatures. In a later version, the function remains equal to one if the temperature is above the optimal temperature. An increase in photorespiration at high temperatures reduces NPP, and at high temperatures other interactions reduce GPP significantly. Carbon dioxide concentration and water availability act in concert to control GPP, with higher CO_2 and H_2O allowing higher photosynthetic rates. The actual curve follows Michaelis-Menton kinetics. The TEM predicts that under a doubled-CO_2 scenario GPP will increase the most in arid re-

gions. Finally, nitrogen availability can limit GPP if the C:N ratio is above that expected for the vegetation type in question. This was an addition to the original model (McGuire *et al.* 1992).

Maintenance respiration (R_m) is calculated using the following equation:

$$R_m = K_r (C_v) e^{(r_T) T}$$

where K_r is the respiration rate of the vegetation on a per gram basis at 0°C, C_v is the mass of vegetative carbon, T is the monthly air temperature, and r_T is the instantaneous rate of change in respiration. The value of r_T is based on a Q_{10} which varies depending on the temperature range in question. In other words, the value of Q_{10} between 0°C and 5°C decreases linearly from 2.5 to 2.0, is equal to 2.0 between 5°C and 20°C, and between 20°C and 40°C it again decreases linearly from 2.0 to 1.5. A third-order polynomial was then fit to these targets to create a smooth function. When maintenance respiration is greater than or equal to GPP, growth respiration is set to zero. Otherwise 20% of the excess GPP is considered to be growth respiration. The above information on photosynthesis and respiration rates is the modelers mathematical summary of the best information available in the literature. The specific curves for each vegetation type are based on field studies in appropriate regions of the world.

Carbon and nitrogen interactions in the first version of the model were quite simple: the carbon to nitrogen ratio was set as a fixed target. If this target was not met, then either more nitrogen uptake would be necessary before carbon assimilation could continue or if nitrogen were not limiting, then carbon fixation would proceed unchecked by the nitrogen supply (Raich *et al.* 1991). An updated version allows the carbon to nitrogen ratio to fluctuate with the season and successional stage (McGuire *et al.* 1992). In the later version, the effect of nitrogen availability is assumed to be parabolic, with the function set equal to one at levels of nitrogen availability which are allow a C:N ratio less than or equal to the "target" C:N ratio for that vegetation type. As nitrogen stress increases, the function decreases along a parabola to zero at a point denoted as $CN_{max.}$ In the most recent version, nitrogen is recycled from senescing tissue.

Other fluxes explicitly simulated include litter losses of carbon and nitrogen from the plant compartments to the soil, heterotrophic respiration (carbon from soil to atmosphere), nitrogen uptake by plants and net nitrogen mineralization. Litter production includes above- and below-ground. Litter loss of carbon is assumed to be equal to NPP, another manifestation of the equilibrium nature of this model. Litter loss of nitrogen was initially calculated to maintain the target C:N ratio in the vegetation, however more recent versions calculate a monthly litter nitrogen value as 1/12th of the

annual nitrogen uptake divided by the mean annual nitrogen content of vegetation (McGuire *et al.* 1992). The heterotrophic respiration flux encompasses all aspects of organic matter decomposition. It is calculated as a function of soil carbon content, mean air temperature, mean soil moisture, and a vegetation type-specific decomposition rate. Temperature which is used to describe a Q_{10} of 2.0 for all temperatures, and moisture availability is a different function for each of the five soil texture classes

Nitrogen uptake is considered to be a function of available soil N (nitrate, nitrite, and ammonium), soil moisture, mean air temperature, and the effect of nitrogen stress in the plants. This results in the parabolic decrease in GPP as described above. Lacking information on gross nitrogen immobilization and gross nitrogen mineralization for each of the vegetation types, the authors chose to use empirical relationships for net mineralization based on the C:N ratio in the soil and empirically derived rate constants. Finally, nitrogen inputs and losses are set to a constant value for each of the vegetation types.

Applications and prospects for the future

Since the TEM is so new, it has only been applied to a few situations. The first application was the creation of a NPP map of South America (Raich *et al.* 1991). This only pertained to the potential vegetation of the continent, since the model is incapable of handling immature plants and succession explicitly. An application to North American NPP followed. This study investigated the interactions between carbon and nitrogen and led to improvements in that part of the model (McGuire *et al.* 1992). The following year, *Nature* published an investigation of global NPP using the output of four different general atmospheric circulation models as the input to TEM (Melillo *et al.* 1993). Dry and tropical ecosystems were predicted to have the greatest direct effect from a carbon dioxide doubling, while moist and northern ecosystems would be affected the most by predicted temperature changes. Most recently, the TEM has been compared with other models. McGuire *et al.* (1993) compared it to the regression-based Osnabruck Model. They found that under a doubled-CO2 scenario, the TEM predicted smaller (2.5% vs. 12.5%) increases in NPP than the regression-based model. This they attributed to explicit treatment of multiple limitations on GPP and feedbacks among temperature and nitrogen availability, photosynthesis, respiration, and available moisture. Most recently, the TEM was included in the VEMAP project mentioned previously.

Future improvements planned for the model include explicit treatment of phosphorous (important in tropical ecosystems), air humidity and windspeed, and the use of a daily time step. A more challenging issue is that of spatial heterogeneity of soils and vegetation. The first step will probably be mathematically parameterizing the heterogeneity at a sub-grid scale, rather than decreasing the

grid scale and consequently increasing the computational demands. The planned inclusion of trace gas fluxes will necessitate the inclusion of wetland cells, since methane production there is so important. Finally, the authors plan to develop methods to include disturbance and succession explicitly. This will increase the utility of the model greatly, since so much of the planet is currently managed for agriculture and silviculture. The inclusion of pest effects are unlikely since the scale of analysis is so small. However, the integration of a process-based global ecological model such as the TEM with general atmospheric and oceanic circulation models is likely to produce more realistic predictions of the effects of climate change and land use patterns on terrestrial ecosystems. The output of models such as TEM could prove valuable as input for pest management models. This is particularly true for modelers who are interested in investigating the potential effects of global change on pest outbreaks.

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Appendix A: Characteristics of Selected Models

Table 1:

Model Class	Model Acronym[a]	References	Temporal Scale[b]	Spatial Scale/ Geographic Use[c]	Plant Aggregation Level	Input Requirements[d]	Primary Objective or Output
Physiology-based	BIOMASS	McMurtrie *et al.* 1990a, 1990b McMurtrie and Landsberg 1992 McMurtrie *et al.* 1992 McMurtrie 1993 McMurtrie and Wang 1993	1 day (diurnal)[e] months-years	-- Canberra, Australia	3 canopy layers, as well as horizontal heterogeneity	nitrogen concentration of leaves	Forest growth (carbon budget) and water budget
Physiology-based	BIOME-BGC[f] FOREST-BGC	Running and Coughlan 1988 Running and Gower 1991 Running and Hunt 1993	1 day & 1 year[g] 50 years	1 hectare 1 hectare to the lower 48 states	Lifeforms = functional types + climate zones	LAI, daily climate data, species-specific data	Carbon, nitrogen, and water budgets
Physiology-based	ECOPHYS	Host *et al.* 1990 Rauscher 1990	1 hour days	individual tree	Individual leaves	Leaf microenvironment, leaf orientation & area, hourly radiation, temp., clonal morphology, and genome	Photosynthate production in jvenile *Populus*
Physiology-based	FORGRO	Mohren 1987 Mohren and Bartelink 1990	1 day (diurnal)[h] months-years	-- Netherlands forest stands	vertical and horizontal spatial variation considered	LAI, needle distribution and orientation	Forest growth, water, C, N, and P cycling, needle mortality
Physiology-based?	INHIBSIM	Knudsen and Hudler 1987				Temp., leaf wetness	Efficacy of biocontrol on fungi infecting *Pinus resinosa*
Physiology-based	MAESTRO	Wang 1988 Dick *et al.* 1990a, 1990b Baldwin 1993	1 hour days	-- Wisconsin	vertical and horizontal spatial variation considered	Hourly humidity, radiation and temperature	Canopy assimilation and transpiration, effect of cones on assimilation
Physiology-based	PGEN	Friend 1991					Photosynthesis and stomatal conductance
Physiology-based	ROOTSIMU	Blake and Hoogenboom 1988	1 day or less Years	-- Alabama	Woody tissues, suberized and non-suberized roots	Climate data, soil data, species-specific data	Root growth and survival
Physiology-based	SPUR	Angell and Miller 1994	-- Several years	-- Oregon juniper rangelands	Individual plants	Air and soil temp., vapor pressure deficit, solar radiation	Stomatal conductance and soil water potential
Physiology-based	TCX[i]	Bonan 1991 Bonan 1993	1 day 10 years	-- Boreal forests	Species	Climate, species-specific data	Carbon balance of boreal forests, N cycle
Physiology-based	TREGRO	Laurence *et al.* 1993 Schaefer and Krieger 1994	-- 10 years	-- South China	Individual seedlings and mature trees	Climate data, soils data	Growth of *Picea rubens* seedlings and saplings, ozone effects
Physiology characteristics empirically determined		Anisko *et al.* 1994		-- Georgia	Species (*Acer, Betula, Liquidambar, Fraxinus, Prunus, Quercus*)	Max., min., & avg. temps.; hourly chill & heat; day length; & date	Empirical cold hardiness of selected hardwood species
Physiology-based and Population	HYBRID[j]	Friend *et al.* 1993	1 day & 1 year[k]	-- Montana and Tennessee stands	Individual trees	Daily climate, species-specific data, species composition of stand	A merger of FOREST-BGC, ZELIG, and PGEN
Physiology-based and Population	LINKAGES	Pastor and Post 1985 Pastor and Post 1986 Stump and Binkley 1993		-- Eastern hardwood forests, Colorado stands			Effect of climate change on species composition of hardwood forests

Table 1:

Model Class	Model Acronym[a]	References	Temporal Scale[b]	Spatial Scale/ Geographic Use[c]	Plant Aggregation Level	Input Requirements [d]	Primary Objective or Output
Population	JABOWA[1]	Botkin *et al.* 1972a, 1972b	1 year decades-centuries	1/100th hectare Hubbard Brook	Individual trees	elev., soil depth, field capacity, %rock in soil, monthly temp. and precip., and annual insolation, species specific data	The original individual-based model for simulation of population dynamics in a stand
Population	FIRESUM	Keane *et al.* 1990		-- Northwest and Rocky Mountains	Individual trees		Succession and yield given fire or pest infestation events
Population	FORENA	Solomon 1986	1 month centuries	-- Eastern USA	Individual trees	Monthly climate, carbon dioxide, species-specific data	Prediction of future vegetation trends with climate change
Population	FOREST-TUNDRA	Sirois *et al.* 1994			Individual trees	Temp., seed input, fire frequency	Seed regeneration of *Picea mariana* at treeline in NE Canada
Population	FORET	Shugart and West 1977 Shugart 1984	1 year centuries	1/12th hectare Anderson County, Tennessee	Individual trees	elev., soil depth, field capacity, %rock in soil, monthly temp. and precip., and annual insolation, species specific data	A modification of JABOWA increased # species to 33, added vegetative reproduction, other improvements
Population	FORFLO	Pearlstine *et al.* 1985 Liu and Malanson 1992 Malanson and Kupfer 1993		Stands in the Midwest USA	Individual trees	Climate, river flow, soil type	Population dynamics and nutrient cycling of riparian stands
Population	FORNUT	Harwell and Weinstein 1982					Pollution effects
Population	PTAEDA PTAEDA2	Webb and Burkhart 1988 Baldwin 93		Stands in the SE USA	Individual trees		Growth and yield of Loblolly Pine, pollution effects
Population	SILVA	Axelrod and Kercher 1980		Western coniferous forests			Pollution effects on growth and succession
Population	STELLA	Wu and Vankat 1991	-- Decades to centuries	-- Broadleaved stands in urban and agricultural areas	Individual trees	Climate data, spatial data describing fragmentation	Succession in fragmented landscapes
Population	ZELIG	Burton and Urban 1990 Urban *et al.* 1991	1 year		Individual trees	Climate, species-specific data	Succession
Population and Ecosystem/ Tissue	FORCLIM[m]	Bugmann 1994 Bugmann *et al.* 1994 Fischlin *et al.* 1994	1 month 100-1000 years		Species-specific age cohorts, individual trees		
Population/ and Ecosystem/Tissue	FORCYTE[n]	Kimmins and Scoullar 1979 Kimmins and Scoullar 1981 Kimmins and Scoullar 1983 Kimmins *et al.* 1988	1 year Decades-centuries	1 hectare Relatively generic	Individual trees, 5 nutrient compartments	Species-specific growth curves, soil parameters	Tracking nutrient status of up to 5 nutrients under varying treatments
Ecosystem/ Tissue	CENTURY-forest	Parton *et al.* 1987 Schimel *et al.* 1990 Sanford *et al.* 1991 Metherell *et al.* 1994	1 month 100-1000 years	1 square meter 1 hectare to regions, see Burke *et al.* 1991, below	C_3/C_4 differentiated; leaves, fine roots, coarse roots, branches, wood, 3 soil organic matter pools	Monthly climate, soil data, species-specific data	Soil organic carbon and nitrogen; C,N,P, and S dynamics
Ecosystem/Tissue	FORECAST	Kimmins *et al.* 1990		Ecosystem-level			Prediction of growth and yield, economics, energy, and wildlife

Table 1:

Model Class	Model Acronym[a]	References	Temporal Scale[b]	Spatial Scale/ Geographic Use[c]	Plant Aggregation Level	Input Requirements[d]	Primary Objective or Output
Ecosystem/ Tissue	FORTNITE	Aber *et al.* 1978 Aber *et al.* 1979 Aber and Melillo 1982		Ecosystem-level			Carbon and nitrogen cycling in forests
Ecosystem/ tissue	MBL-GEM[e]	Rastetter *et al.* 1991 Rastetter *et al.* 1992	1 month and 1 year[p] 50 years	Ecosystem-level Forest stands	Plant Communities (foliage, fine roots, stems)	Climate data, carbon dioxide, fertilization	C/N ratios in plants and soils in response to climate change
Ecosystem/tissue	NuCM[q]	Liu *et al.* 1991	1 week	Ecosystem-level New York and Tennessee			Biogeochemistry of soils, vegetation, litter, water, acid rain
Ecosystem/ Tissue	PnET-CN	Aber and Federer 1992	1 month	Ecosystem-level Temperate and boreal forests	Foliage, wood, and fine roots	Climate data, soil data	Prediction of production and allocation of carbon
Ecosystem/ Tissue	Q[r]	Bosatta and Ågren 1991a, Bosatta and Ågren 1991b Rolff and Ågren in press	1 year Decades to centuries	Ecosystem-level	Trees vs. other plants, but not individuals Foliage ages; branches, stems, coarse roots, and fine roots	Substrate quality, biochemical parameterization of the plant components	Originally developed to evaluate nutrient effects of whole-tree harvesting Also used to evaluate global change effects
Ecosystem/ Tissue		Mitchell *et al.* 1975 Waide and Swank 1975 Waide and Swank 1977		Ecosystem-level			
Regional ecology/ Atmosphere	LEAP[s]	Goudriaan 1989 Avissar and Pielke 1989 Lee 1992	-- Equilibrium solutions	20 km x 20 km Eastern Colorado	Functional type	Surface energy budget, plant distribution	Ecosystem-atmosphere interactions, esp. transpiration
Regional ecology	CENTURY & a Geographical Information System	Burke *et al.* 1991	1 month 50 years	1 square meter Central US Great Plains (600 km x 800 km)	C_3/C_4 differentiated; leaves, fine roots, coarse roots, 3 soil organic matter pools	Monthly climate data, soil texture, relative amount of C_3/C_4 plants	Equilibrium solution to climate change for the US Great Plains
Regional/ Integrated	DYNARIP	Bechtold 1984		Stands Stands, states and regions	Forest cover types	Empirically determined transition matrix	Predicts future status of forests in a region based on 27 disturbance types
Regional/ Integrated	IPASS[t]	Maki *et al.* 1985 McHugh *et al.* 1989		Not explicit Alaska, but can be generic	Human communities and ecosystems	Demand for goods and services, availability of capital and labor	Policy analysis in Alaska
Regional/ Integrated		Dale *et al.* 1993 Southworth *et al.* 1991					Land use in Rondonia, Brazil and carbon cycles effects
Regional/ Integrated		Lee *et al.* 1992					Integration of economics, land use, and ecology
Regional/ Integrated		Turner 1987 Turner 1988	-- Years to decades	County Georgia			Prediction of land use changes in Georgia
Global ecology/ Atmosphere	BATS[u]	Dickinson 1985 Dickinson *et al.* 1986	-- Currently only equilibrium solutions	400 km x 400 km Continental to the Biosphere	All plants lumped	Surface energy budget	Provides a surface parameterization for atmospheric general circulation models
Global ecology/ Atmosphere	SiB, SiB II, SSiB[v]	Sellers *et al.* 1986. Xue *et al.* 1991	1 month Currently only equilibrium solutions	400 km x 400 km Continental to the Biosphere	Trees and ground cover have separate transpiration rates	Surface energy budget, LAI	Provides a surface parameterization for atmospheric general circulation models

Table 1:

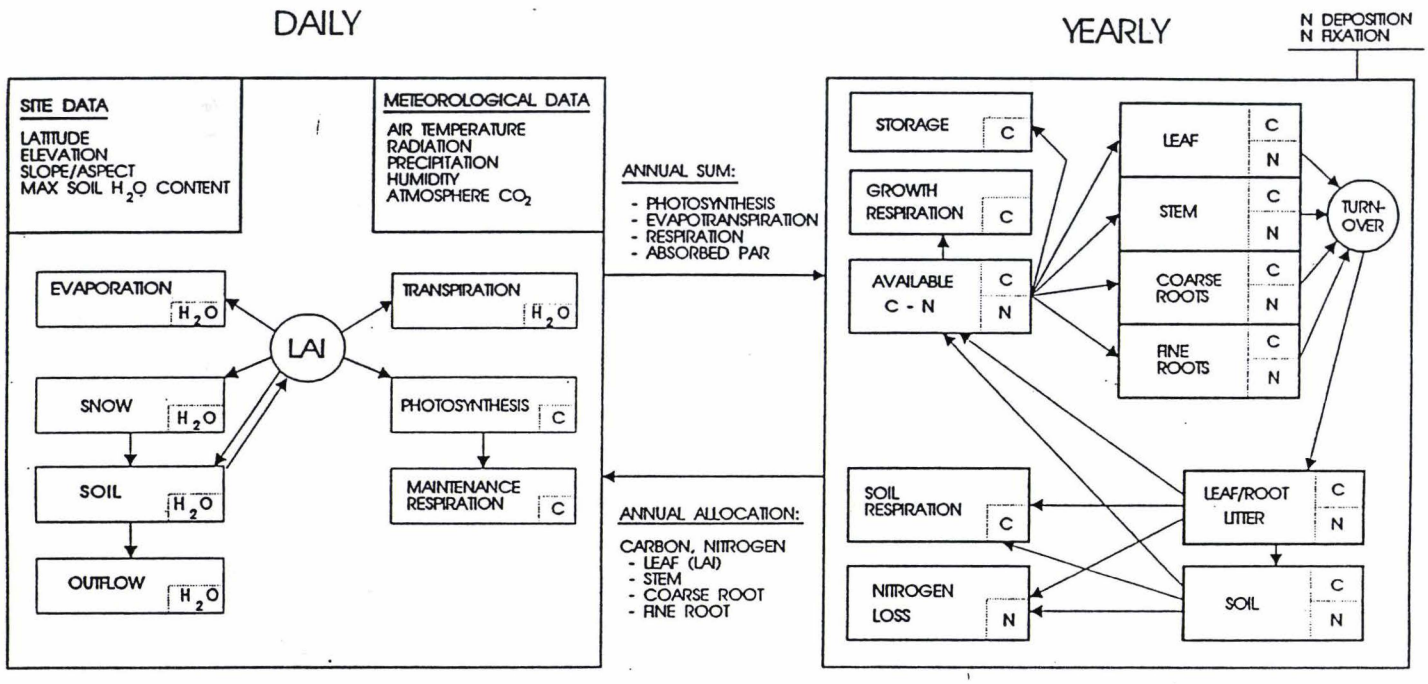
Model Class	Model Acronym[a]	References	Temporal Scale[b]	Spatial Scale/ Geographic Use[c]	Plant Aggregation Level	Input Requirements[d]	Primary Objective or Output
Global ecology/ Biome distribution	TEM[w]	Raich *et al.* 1991 McGuire *et al.* 1992 McGuire *et al.* 1993 Melillo *et al.* 1993	1 month ~ 100 years for equilibrium	0.5° x 0.5° Continental to the Biosphere	18 Different Vegetation Types	Climate, soils, vegetation type, elevation	NPP in relation to climate change scenarios, C/N dynamics
Global ecology/ Biome distribution		Box 1981 Cramer and Leemans 1992	-- Equilibrium[x]	-- Continental to the Biosphere	100 Functional types	Climate	Equilibrium biome distribution
Global Ecology/ Biome distribution		Emanuel *et al.* 1985a Emanuel *et al.* 1985b		-- Continental to the Biosphere	see Ågren 1991	Climate	Equilibrium biome distribution
Global Ecology/ Biome distribution		Prentice *et al.* 1992	-- Equilibrium	0.5° x 0.5° The Biosphere	Functional types	Climate	Equilibrium biome distribution under climate change

a. Many of the full names or etymology are noted below.
b. The first number(s) refers to the smallest time-step on which the model is run and the second set of numbers characterizes the time frame of the simulations that are typically carried out using the model.
c. The first number refers to the smallest unit explicitly modeled if one exists, and the second number or phrase characterizes the sizes and/or areas for which this model has been used. This does not necessarily indicate that the model can or cannot be used in the other areas.
d. Ideally, this category will characterize the type of input necessary, but it may simply point out unusual and specific input requirements.
e. The time step for BIOMASS is daily, but aspects of the diurnal meteorology are incorporated in the calculation of total photosynthesis and transpiration.
f. Name derived from BIOME-BioGeochemical Cycling, and its predecessor FOREST-BioGeochemical Cycling.
g. BIOME-BGC utilizes a dual time step; 1day for hydrology canopy gas exchange, and maintenance respiration; and 1 year for carbon allocation, decomposition, and the nitrogen cycle.
h. The time step for FORGRO is daily, but aspects of the diurnal meteorology are incorporated in the calculation of total photosynthesis and transpiration.
i. Terrestrial Carbon eXchange
j. Name derives from the model being a HYBRID between FOREST-BGC, a physiology-based model and ZELIG, a population model.
k. HYBRID, like BIOME-BGC has a dual time step; 1 day for carbon uptake and respiration as well as transpiration; 1 year for carbon allocation and resultant diameter growth.
l. Named after the authors, JAnak, BOtkin, and WAllis
m. FORest simulation in a changing CLIMate.
n. Name derived from FORest nutrient CYcling and Yield Trend Evaluator.
o. Marine Biological Laboratory's General Ecosystem Model.
p. PnET-CN uses a monthly time step for all processes except carbon allocation to wood and fine roots, which is carried out at the end of each year.
q. NUtrient Cycling Model
r. Name derived from a key variable, substrate Quality.
s. Land Ecosystem Atmosphere Feedback model.
t. Interactive Policy Analysis Simulation System
u. Biosphere-Atmosphere Transfer Scheme.
v. SImple Biosphere model and its descendents.
w. Terrestrial Ecosystem Model
x. A time step is not explicitly used in these models as they determine an equilibrium solution.

Appendix B: Flowcharts

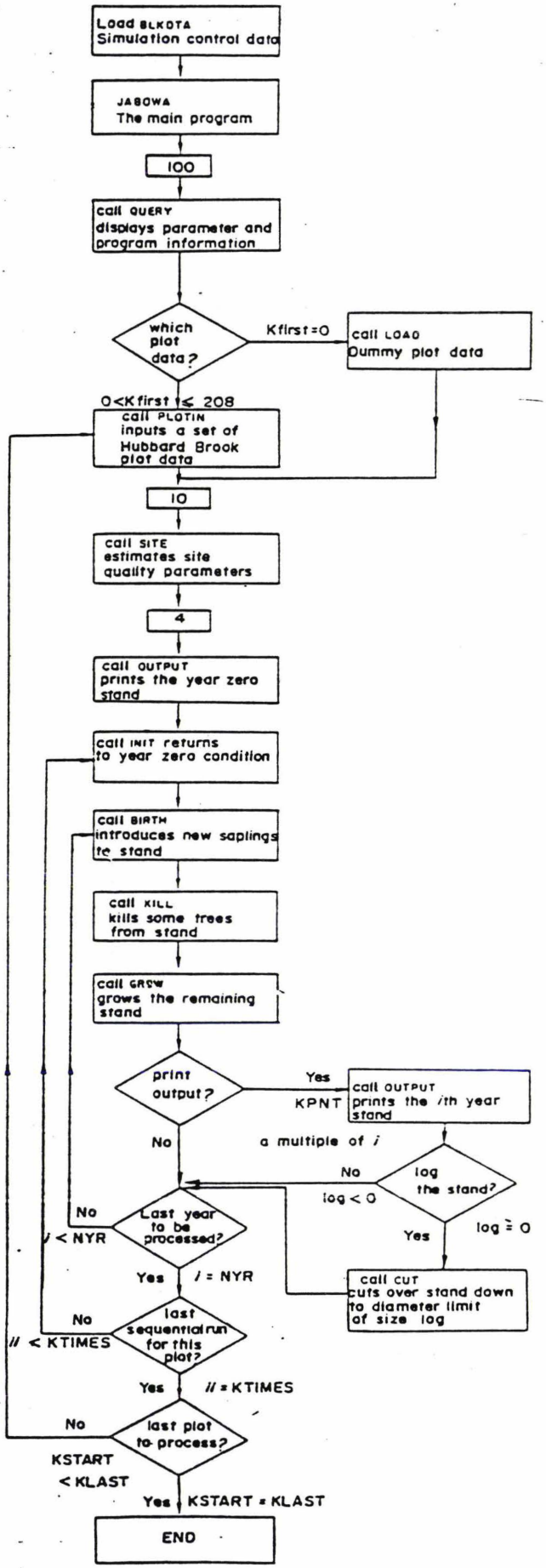
BIOME-BGC

(Hunt 1993)



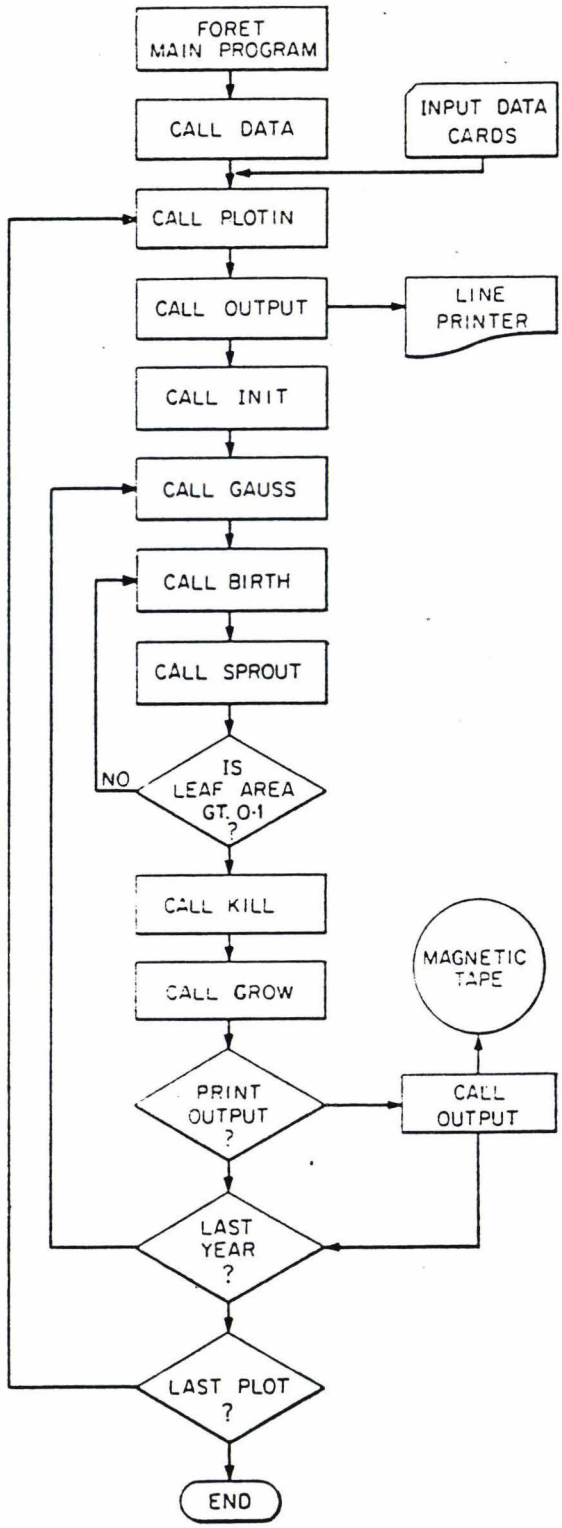
JABOWA

(Botkin *et al.* 1972a)



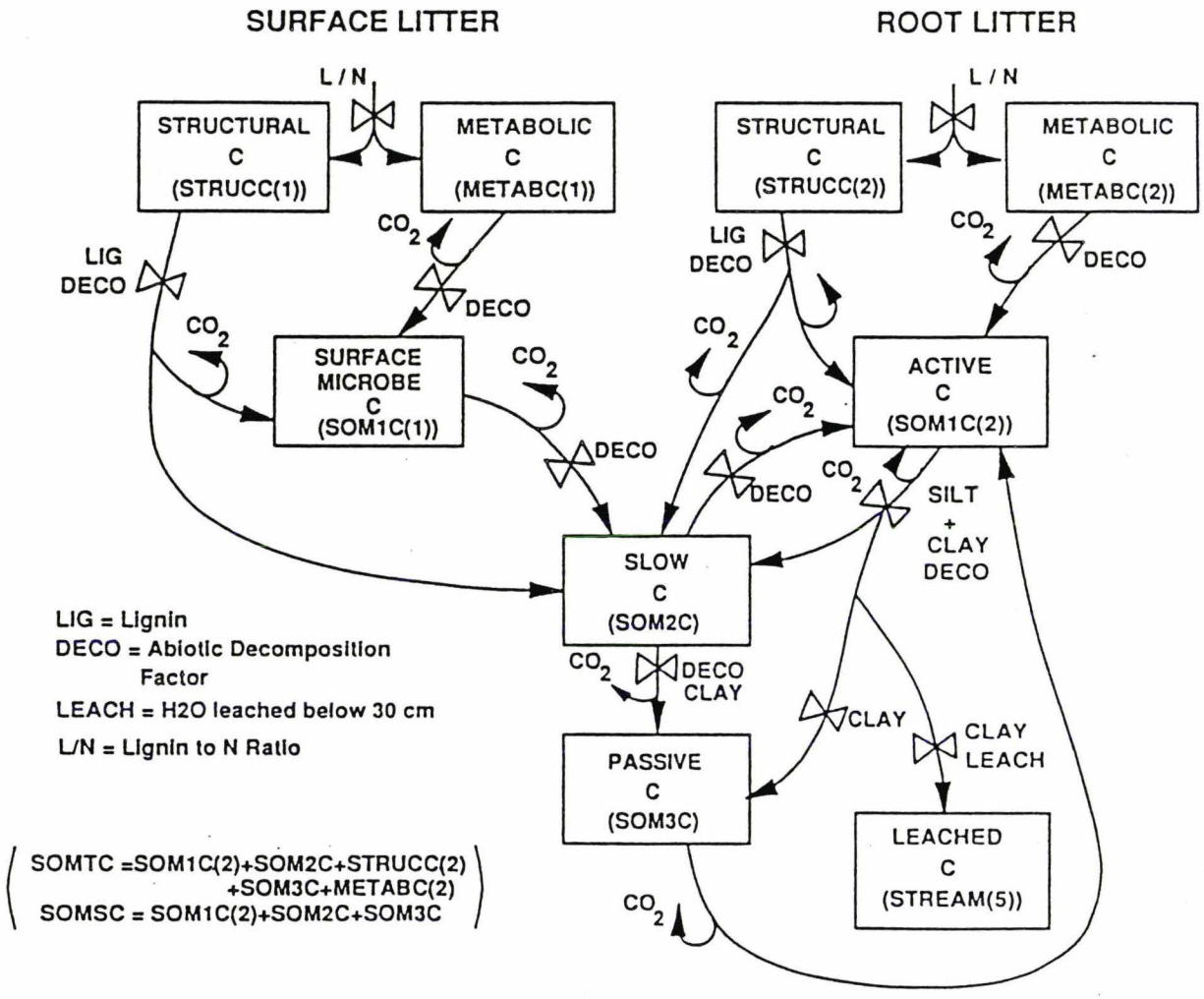
FORET

(Shugart and West 1977)

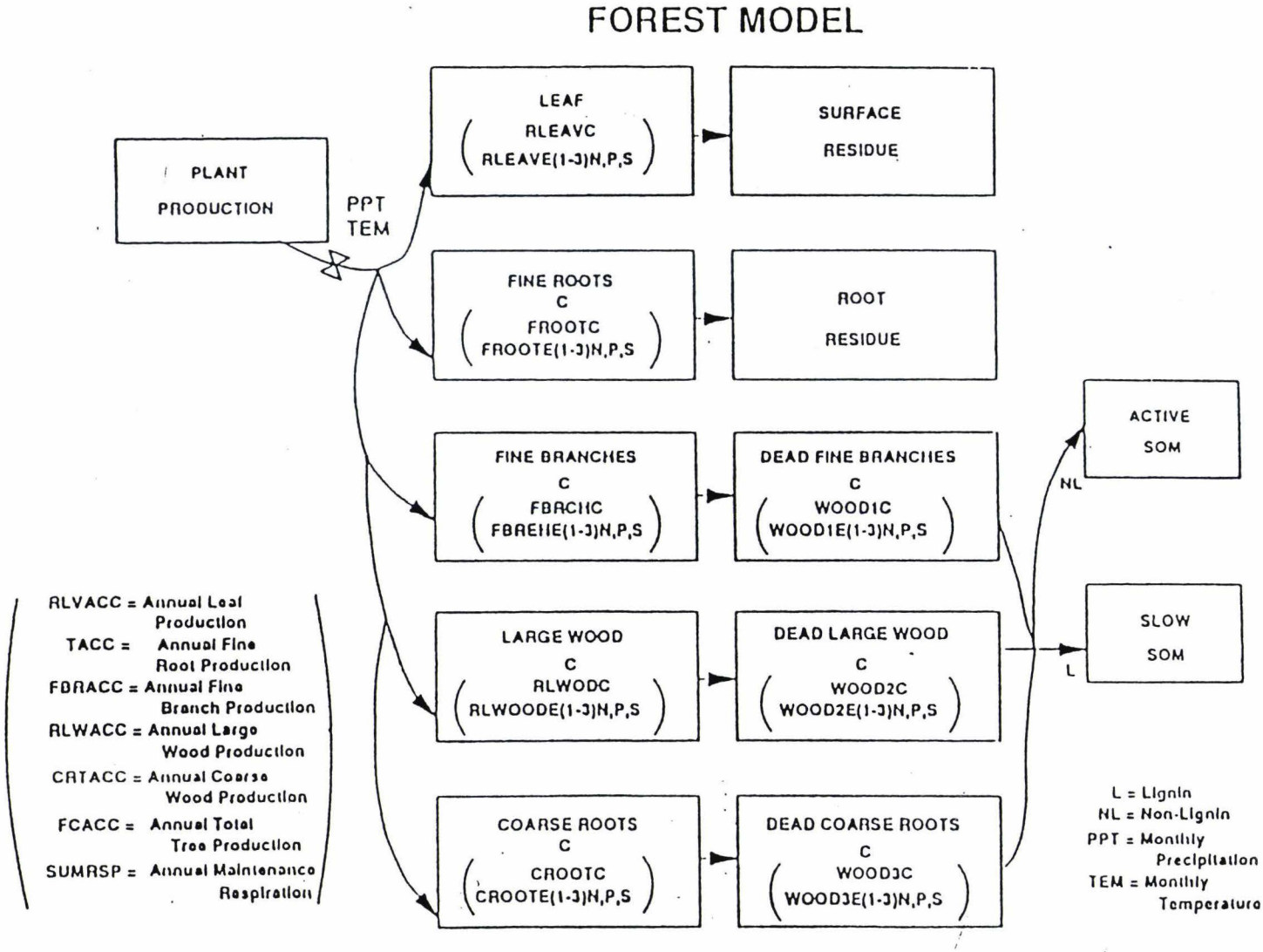


CENTURY

Soil Organic Matter Submodel
(Parton *et al.* 1987)

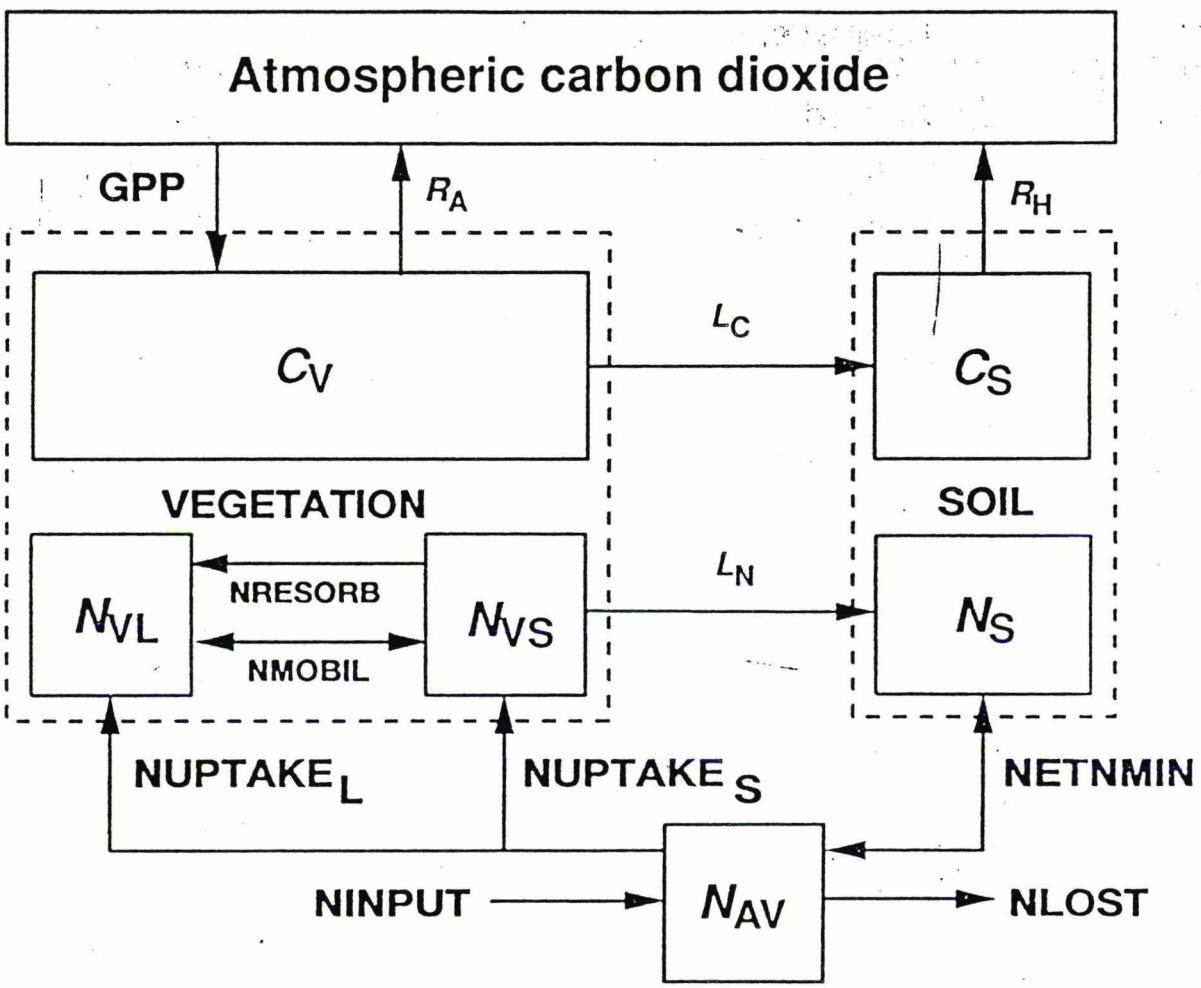


Forest submodel
(Sanford et al. 1991)



TEM (Terrestrial Ecosystem Model)

(Melillo *et al.* 1993)



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